THE

JOURNAL OF ECOLOGY

VOLUME XXI

THE
JOURNAL OF ECOLOGY

EDITED FOR THE

BRITISH ECOLOGICAL SOCIETY

BY

A. G. TANSLEY

VOLUME XXI

1933

WITH TWENTY-TWO PLATES, AND NUMEROUS
FIGURES IN THE TEXT

CAMBRIDGE
AT THE UNIVERSITY PRESS

1933

CONTENTS

THE TERMINOLOGY OF "XEROPHYTISM"

By D. THODAY.

THE problem of "xerophytism" has attracted renewed attention lately with the accumulation of a large amount of experimental data by Maximov and his associates, by Huber, Stocker, Walter, Seybold and others. These data have made it clear that xerophytes are not necessarily characterised by a low rate of transpiration, and have brought out more prominently the diversity of types included among them.

How the old terms are to be fitted to the new outlook has been repeatedly discussed in the recent literature. The positive suggestions, however, are somewhat divergent, and the moment seems opportune for an attempt to secure uniformity before usage has become confused.

Much of the difficulty has been due to the fact that the concept "xerophyte" came to include certain characteristics of form and structure as well as of habitat. This limited the application of the term in a manner which was rather arbitrary and never clearly defined.

It was applied at first quite generally to plants growing in dry localities (**13**). This seems indisputable. Schimper (**12**, p. 2) states: "It is usual to designate the plants...of dry localities as xerophytes," and goes on to extend the meaning of dryness to cover physiological dryness. "Xerophilous" was used by de Candolle, and by Warming (**19**, p. 36) in suggesting a modification of de Candolle's definition, with reference to habitat.

Schimper, however, made the categorical statement (*loc. cit.* p. 4) that "all plants with an environment" which is physiologically dry "possess the structure and characteristics of xerophytes." This statement is ambiguous. If the environment has already been classed, quite independently, as dry, then it means that a study of the plants growing in the locality in question will reveal to us the structure and characteristics of particular xerophytes. If, on the other hand, xerophytes are to be defined by structural features the statement is inaccurate in its universality, and involves the fallacy: Many xerophytes show features of certain kinds which are therefore called xerophytic; xerophytic features are characteristic of xerophytes; plants without such features are not xerophytes. As Maximov says (**11**, p. 25): "Many authors have assumed that features peculiar to some special class of xerophytes are characteristic of the group—in reality a very diverse one—as a whole." Yet although structural implications have become associated with the term, it has always referred primarily and principally to the dryness of the habitat.

Emphasis of the protective effect of many xerophytic characters against loss of water, resulted further in the inclusion of reduced transpiration within the concept. This is most clearly seen in the categorical statement in Benecke and Jost's *Pflanzenphysiologie* (**2**, vol. I, p. 82): "Die Pflanzen trockener

Standorte, die Einschränkungen in der Transpiration aufweisen, nennt man Xerophyten." It led Kamerling (**9**) to exclude as "pseudoxerophytes" plants usually regarded as most typical of dry habitats, because he found that they transpired rapidly. The fact that he has not been followed shows that reduction of transpiration was less fundamental to the concept than the other parts of its connotation.

The view of "xerophily" as a "natural concept involving the total reaction of plant to environment" and not to be defined "in terms of habitat, of anatomy, or of physiology alone," was ably put by Delf (**4**) in 1915; but a perusal of her paper leaves the impression that the facts already known were showing the anatomy and physiology to be very diverse. The only consistent feature of the concept was therefore that of habitat. The reference to anatomy and physiology implied nothing more definite than that plants are adapted to their natural environment.

The term "xerophytic," as applied to adaptations, was brought into disrepute by the difficulty that so-called xerophytic features are not confined to plants of dry habitats. Schimper had met this difficulty in part by distinguishing between physical and physiological drought; but many facts have accumulated since, which this view is inadequate to cover (cf. e.g. Delf (**4**), p. 113, on halophytes).

The difficulty has been avoided by the use of "xeromorphic" instead of "xerophytic." This term, which has come into general use, has the advantage that it is applicable to plants that are not xerophytes. Broadly it signifies "having features such as are characteristic of xerophytes"; but it has not remained uncontaminated by the "reduction of transpiration" taint. Warming (**19**) defined it as "protected from desiccation by certain devices," which he enumerated.

Maximov (**11**, p. 372) has recently suggested that "xeromorphic" should be used for those features of form and structure which can be shown by experiment to be produced or intensified by desiccating conditions. An appreciation of the similarity between many xeromorphic features and the structural effects experimentally produced by such conditions was shown by Schimper (**12**, pp. 4–7) and by Warming (**19**, pp. 127–30). Nevertheless Maximov's proposal is open to the objection that it is a departure from current usage, makes no provision for data not yet causally analysed and may lead to confusion. Some plants are relatively non-plastic and their xeromorphic features are hereditary—in fact, this is in a high degree true of very many xerophytes. We cannot assume without begging a big question that these features have been directly due to environmental influences in the past history of the species and therefore they do not strictly come under Maximov's definition[1]; yet we need

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[1] "Wie weit die 'xerophilen' Einrichtungen der Blätter von den Aussenbedingungen (besonders Luft- und Bodentrockenheit) abhängen und durch sie hervorgerufen oder geändert werden, oder wie weit unabhängig hiervon feste erbliche Merkmale (also keine 'kausalen Funktionsharmonien,' wenigstens nicht in der Gegenwart, hypothetischerweise höchstens im Lauf der Stammesentwicklung) vorliegen, bedarf freilich noch eingehender Untersuchungen." **Ungerer** (**17**), p. 110.

a term to cover them. Rather than find a substitute for "xeromorphic" in its customary sense, it would be better to find a new term for features coming within Maximov's category. "Xeroplastic" may be suggested as more appropriate in its literal significance.

Xeroplastic features (examples of "xeromorphosis," cf. Ungerer (**17**, p. 99)), as shown in the experiments of Zalenski, Yapp, Alexandrov and others (**11**) for particular species, are in general xeromorphic; but when similar features are exhibited by a given desert plant they cannot be assumed to be xeroplastic until experiments with that species have demonstrated them to be so.

Since sun leaves as compared with shade leaves show similar features (cf. Huber, **6**, etc.) it may theoretically be desirable to distinguish between xeroplastic and helioplastic characters. It is doubtful, however, whether a sharp separation is possible, even in theory.

If xeroplastic is accepted for Maximov's category, "xerophyte" and "xeromorphic" can retain their customary significance; but they require clearer definition.

The difficulties to which reference has so far been made could be avoided and historical continuity maintained by using "xerophyte" to mean a plant growing in a dry habitat, irrespective of the kind of adaptations it exhibits. Like Warming's "eremophyte," etc., it would have simply a habitat significance, with no particular functional or structural implications. It would be a relative term. Authors are generally agreed that the boundaries of this class cannot be sharply drawn.

"Xeromorphic," on the other hand, has replaced "xerophytic" as used in a rather restricted sense, to characterise those features *of the aerial shoot system* which are exhibited in a marked degree by conspicuous xerophytes— i.e. those which stand out as different from "ordinary" plants, give xerophytic vegetation its peculiar facies and strike the eye as distinctive of it.

Some of these xeromorphic features are actually such as reduce the water loss to a minimum in emergency. Some of them do reduce water loss (e.g. cuticular transpiration) at all times *in comparison with an imaginary plant similar in all respects but lacking these features*. Indeed, when the functional effects of anatomical characters are considered, they are generally taken one at a time and the effect estimated *ceteris paribus*. This is probably as far as Schimper went when he emphasised the reduction of transpiration in xerophytes.

Experience has taught us the dangers of inference from mere anatomy, even with regard to how structures work (the limitations of stomatal control are a case in point) and especially from xeromorphy to physiological drought. Therefore it is not justifiable to attach a functional significance to the term "xeromorphic" any more than to "xeroplastic." Xeromorphic should be purely comparative-morphological, xeroplastic purely causal-morphological. Moreover they are descriptive, not classificatory: e.g. xeromorphic and halomorphic

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are not mutually exclusive; the development of water tissue may be xeroplastic (**1**) *or* haloplastic; and similarly with xeromorphic and heliomorphic, etc.

The one limitation which would historically be justified is that xeromorphic should apply to the aerial, transpiring system only, not to the underground parts, or, for example, to the balance between the transpiring and absorbing systems.

This still leaves the meaning of "xeromorphic" vague. Maximov aimed at making it more definite. The facts, however, seem to preclude this. It is difficult to find any anatomical characters which are truly *general* among xerophytes. The concept is really a composite one, in which several kinds of xeromorphy are included. Plants with tough leathery leaves, phyllodes or phylloclades, with thick cuticle; or with soft hairy leaves; some of them microphyllous, with leaves flat or grooved; plants with rudimentary leaves, switch plants or stem succulents; leaf succulents—in diverse combinations these contribute to give vegetation a xeromorphic aspect. Closer definition of what is a xeromorphic character could hardly be successful, except within limited groups.

In contradistinction to xeromorphic, "xerophytic" would signify simply "appertaining to a xerophyte." "Xerophytic adaptation" would then be applicable without limitation to any character, not solely of the shoot system, of a xerophyte, which adapts it to a relatively dry habitat. A "xerophytic grass" would mean a grass which is a xerophyte.

"Xerophytic vegetation" in the strict sense would mean vegetation composed of xerophytes, i.e. vegetation of dry habitats, not vegetation with a xeromorphic facies, though xerophytic *vegetation* taken as a whole is by definition predominantly xeromorphic, our idea of what is xeromorphic being derived from those elements in xerophytic vegetation which give it its characteristic facies[1].

The terms have been used substantially as here proposed by Schratz (**14, 15**) and Hüser (**7**), by James (**8**, p. 170) and broadly speaking by Maximov and Huber.

The chief objection to using xerophyte with merely a habitat significance is that expressed very cogently by Walter (**18**), that the habitat may not be equally dry even for two species growing in the same locality. Not only may the conditions vary considerably even within a small area (**10**) but conditions may show stratification above and below ground.

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[1] The term xeric suggested (along with mesic and hygric—hydric is surely a misprint) by **Cooper** and **Weese** (**3**), for a copy of whose article I am indebted to Prof. Tansley, does not seem to offer any clear advantage. That "xerophytic habitat" is tautological may be admitted; but we already have dry, arid and semi-arid from which to choose in characterising habitats. As for the plant, not even a xerophyte can be called xeric with strict propriety, especially if we are also to call the habitat xeric. Literal meanings should not be over-stressed; but in that case why not "xerophilous"? Its literal meaning is hardly a sound guide to its accepted connotation, and even literally it would be less objectionable as applied to animals. Xerocolous avoids the objection, but is a hybrid. Siccocolous is hardly euphonious, nor are mediocolous and humidocolous attractive. In any case, however, the terms adopted should refer to habitat and not to structure.

Inherent in this objection are two implications:

(1) that the habitat which qualifies a xerophyte can or should be more strictly defined;

(2) that certain kinds of adaptations, e.g. a root system deep enough to reach underground water, should disqualify plants possessing them from being classed as xerophytes.

Attempts to restrict in either of these directions the use of a term, which was never intended to be used in any but a very broad sense, will only lead to confusion, as such attempts indeed have led in the past. The progress of knowledge need in no wise be hindered by the retention of convenient terms to cover a wide range of phenomena, even though they must necessarily remain loosely defined, so long as this is clearly recognised. Other terms can be found to embody such new distinctions as the growth of knowledge may demand.

This line of thought is inconsistent with the exclusion of succulents from the category of xerophytes. Recent work has brought into greater prominence the differences between succulents and non-succulents, but does not necessitate or in itself justify confining the term to one of them. In fact, different parts of one and the same plant may be respectively succulent and non-succulent. The wisdom of excluding even ephemerals as such may be doubted, for not all ephemeral species can survive desert conditions. As in the case of succulents, exclusion would amount to discrimination against a particular mode of adaptation.

The remainder, which Maximov calls "true" xerophytes, are still very diverse. The degree of sclerophylly, for example, varies very much among the Mediterranean type of vegetation. On the dry northern slopes of Table Mountain along with sclerophyllous and ericoid types are soft-leaved plants like *Athanasia parviflora*, the dissected leaves of which have a thin cuticle and superficial stomata and are not hairy. On the semi-arid Karroo, *Galenia africana* is neither succulent nor sclerophyll. Physiological as well as morphological diversities are to be expected, as Walter (**18**, p. 104) has found in his attempts to classify xerophytes according to the osmotic pressure of their sap (cf. also H. Evans (**5**) on succulents). Various degrees of drought resistance, in the sense of resistance to lowered water content, exist among "true" xerophytes, correlated with differences in conductivity of wood and extent of root system (cf. Stefanoff and Stoičkoff (**16**)).

The real value of recent work lies in the wealth of detailed knowledge it has provided, based largely on experiment, and the clearer understanding it has made possible of the varied ways in which plants are enabled to survive in dry situations. It has also directed attention beyond the water economy to other important aspects of the physiology of xerophytes.

Nothing in this contribution, it need hardly be said, is intended to belittle the importance of the distinctions that have been drawn, or the attempts that have been made to classify the new data. It has been written solely in the hope

of terminating an old, and now rather barren and obsolescent controversy regarding the use of words.

SUMMARY.

It is proposed to call *xeroplastic* those characters which are developed under the influence of drought, and to retain "xeromorphic" for features of the shoot system such as distinguish the vegetation of dry localities from that of moister localities, without attaching to it any functional significance. Similarly it is proposed that "xerophyte" should not carry any particular functional or structural implication, but be used for plants of dry habitats, irrespective of their modes of adaptation to such habitats.

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A STUDY IN ALTITUDINAL ZONATION IN SOUTH KIGEZI AND ON MOUNTS MUHAVURA AND MGAHINGA, UGANDA

By J. D. SNOWDEN.

(With Plates I and II and one Map in the Text.)

CONTENTS.

THE interesting and picturesque district of South Kigezi, in which I was able to make a short tour during April, 1929, is situated in the south-west corner of Uganda. It lies south of Lake Edward and north of Lake Kivu, being almost midway between the two. The district is bounded on the west by the Belgian Congo, on the south by the Belgian Mandated Ruanda Territory, and on the east by the Ankole district of Uganda.

PHYSIOGRAPHY.

South Kigezi is a mountainous region very little of which is less than
6000 ft. in altitude, while much is over 7000 ft. and some ranges are 8000 ft. or
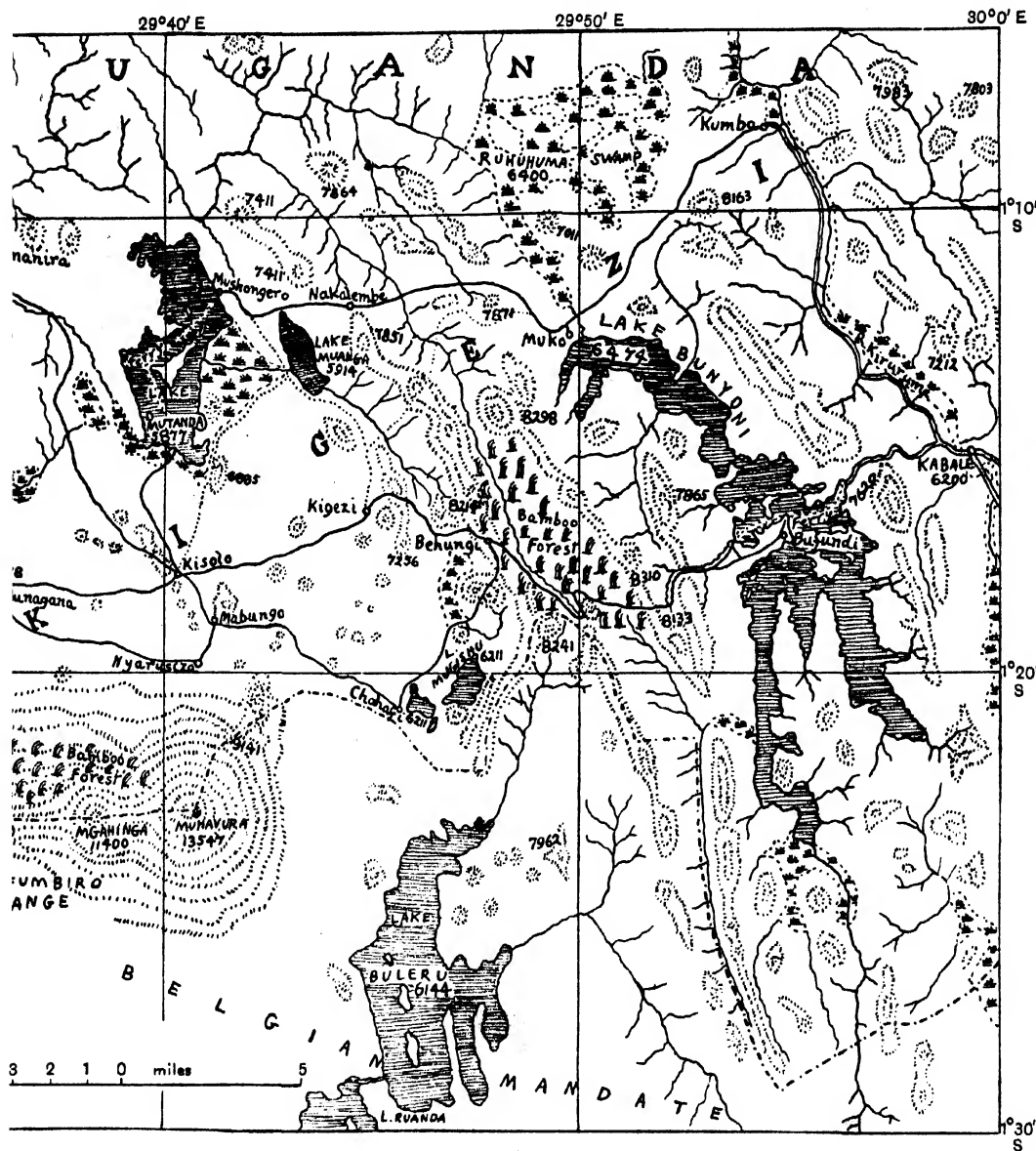
FIG. 1. Sketch map of South Kigezi, Uganda (modified from Africa sheet $\frac{\text{South A 35}}{\text{L}}$, Mufumbiro),
showing mountains, lakes, bamboo forests and swamps. Heights in feet.

more. In the extreme south-west the country is dominated by the three most
easterly peaks of the Mufumbiro or Virunga Mountains, Mounts Muhavura
(13,547 ft.), Mgahinga (11,400 ft.), and Sabinio (11,960 ft.), which mark the

boundary between Uganda and Belgian Ruanda in that district. These mountains, which are of volcanic origin, are separated from the other mountain ranges farther north and east by an extensive rocky lava plain which is dotted here and there with the cones of small extinct craters rising from one to several hundred feet. A number of lakes extend around the edge of this plain, among which are Mutanda (5877 ft.) on the north-west, Muanga (5914 ft.), slightly to the east, and near the southern boundary, east of Mount Muhavura, Mugishu and Chahafi (both 6211 ft.). East of these two lakes rises a high range of hills running in a north-westerly direction across the country, the highest parts of which are over 8000 ft. above sea-level. Beyond this are other ranges, some of which run almost parallel with it and are little less in altitude. Winding in and out between these high mountain ranges to the east is Lake Bunyoni (6474 ft.) the largest lake in South Kigezi.

The country is well watered by numerous rivers, some of which are swiftly flowing mountain streams, though most of the larger ones are sluggish and sometimes spread out into papyrus-filled swamps. Most of the large ones run either north-westerly or south-easterly, with the exception of the River Ruchuru, which first runs mainly westerly before turning north in Belgian territory. This river is fed by the waters of Lake Bunyoni which run into it via the Ruhuma Swamp and Lake Mutanda. The waters from the Kigezi side of Mounts Muhavura, Mgahinga and Sabinio must flow underground to the various lakes, as there are no important surface streams which cross the lava plains.

AREA TRAVERSED.

The route followed from Kabale, the administrative centre of the district, was south-westerly to Bufundi on Lake Bunyoni, then over a couple of high ridges with bamboos in the intervening valley to Behungi (8200 ft.), from which camp a splendid view is obtained of the Mufumbiro Mountains: next southwards across the rocky lava plains to Chahafi near the Belgian Ruanda border, and then westerly to the more fertile areas around Mabungo (6500 ft.). A stay of ten days was made in this vicinity during which Mount Muhavura was climbed and a partial ascent made of Mount Mgahinga. The return journey was made northwards across Lake Mutanda to Mushongero, then easterly across very hilly country via Nakalembe (7500 ft.) to Muko, on the north-west corner of Lake Bunyoni. From here a detour was made around the hills north of the lake to Kumba from which place the road running along the River Kiruruma was followed to Kabale.

SOILS.

The soils are mainly derived from clay rocks of the argellite series and correspond to the Red Loams and Immature Red Loams of Shantz and Marbut in the *Vegetation and Soils of Africa*. The soft clay rocks are often near the surface and in colour range through various shades of reddish brown

to purple and slate blue. They are especially noticeable around the edges of the lakes and on the hill-tops. Quartzite or sandstone rocks are very rarely seen. In the lava plains around Mounts Muhavura and Mgahinga the eastern portion near Chahafi is full of large clinker-like rocks, which are either above or very near the surface, so that the native cultivators have to dig them out and pile them in heaps in order to plant their crops. The westerly portion of the plain is more fertile, as the rocks are generally hidden by a rich, fertile volcanic soil, though in some places it is often mixed with a large proportion of very fine ashes resembling broken coke.

CLIMATE.

At lower altitudes the climate is *subtropical* with the temperature at night not dropping so low as freezing-point. In the next highest zone it may be termed *temperate*, occasional night frosts occurring and the cultivation of ordinary *tropical* crops not being successful. At higher altitudes frosts are more frequent and *subalpine* and *alpine* conditions prevail. Reference will be made to the climate of each vegetational zone under the climatic headings.

PLANT COMMUNITIES.

The vegetation may be divided into several zones which are roughly marked off from each other by increasing altitudes owing to the changes in climate which naturally follow on account of the increased elevation above sea-level. These vegetational zones have very much in common with those at similar altitudes on other East African mountains, and in classifying and describing them references (*Synonymy*) will be given under each heading to some of the Vegetational Regions and Plant Communities previously described which are considered to be closely allied or more or less synonymous with those which are the subject of this paper. The term "formation" is used in approximately Engler's sense. Reference to Phillips's paper in this JOURN. **18**, 219–28, will show that some of the communities he has accepted for Tanganyika do not quite coincide with those I have recognised for Uganda. Where possible the community names of previous authors have been used, but it remains for future workers to decide, after more detailed study, how far they can really be considered under the same terminology.

I. THE EAST AFRICAN MOUNTAIN FOREST FORMATION.

Synonymy. Subtropische Busch-, Gras, und Höhenwaldregion; Engler, 1910, pp. 927–28, 931–34. Der *Gürtelwald*: Volkens, 1897, p. 295. *Kulturzone*: Stuhlmann, 1894, p. 301. *Subtropical Evergreen Forest Formation*: John Phillips, This JOURN. **18**, 1930, pp. 219–28. *Mountain Forest*: Chipp (in Tansley and Chipp, 1926, p. 208).

This formation lies above the *Tropische Regenwaldregion* (Engler, 1910, p. 928) and below the *Subalpine and Alpine Region* (*loc. cit.* p. 935). It is,

however, very extensive, and in order to deal with it more effectively it is here proposed to divide it into (1) a lower *Subtropical Zone* and (2) an upper *Temperate Zone*, into which the vegetation most naturally falls.

(1) The Subtropical Zone.

This is by far the most important and extensive of the several zones and extends from approximately 6000 to 7500 ft. altitude. It is not only found in Kigezi but occurs also on Mount Elgon and on the Highlands of Kenya Colony. It is the area lying between the Tropical Rain Forest and the Bamboo Forest of Engler and other authors. It is characterised by the almost complete absence of palms, its lowest boundary being the highest limit reached by the wild date palm (*Phoenix reclinata* Jacq.), while the upper boundary is marked by the lowest fringe of the hollow-stemmed bamboo (*Arundinaria alpina* K. Schum.) or, on mountains where this is absent, by the presence of *Hagenia abyssinica* Gmel. or *Hypericum lanceolatum* Lam. This subtropical zone is further characterised by the dominance on moist meadowlands of *Pennisetum clandestinum* Hochst. (known as "Kikuyu Grass" in Kenya Colony), a species now well known but probably overlooked by earlier travellers in East Africa on account of its very small flowers being almost concealed in the axils of the upper leaves and only noticeable when the long white stamen filaments, with yellow anthers at the tips, are extruded. In addition this zone includes the highest cultivated lands, as native habitations and cultivations usually cease at about 7500 ft. altitude.

The climate is much less moist and humid than that of the Tropical Rain Forest. Such few statistics as are available for Kigezi give the average annual rainfall as 40 in. per annum and its range as from 35 to 45 in. To make up for this comparatively low rainfall, mountain mists are very prevalent and on some days the sun is scarcely seen at all. The rainfall is usually well distributed throughout the year, though there are two rather wetter and two somewhat drier periods, these latter being generally from the end of December to the end of February, and the end of June to the end of August. The temperature is never tropical, the day temperatures ranging from 70 to 80° F., and the night from 40 to 50°. As an indication of the climate it should be noted that bananas can be grown only in sheltered localities and below 7000 ft. altitude, and the same is true of *Coffea arabica* L.

The following are the largest and most important communities which make up this vegetative zone.

(a) Subtropical Evergreen Forest.

Synonymy. Höhenwald oder Nebelwald: Engler, 1910, pp. 332, 952. *Der Gürtelwald*: Volkens, 1897, p. 295. *Der Gebirgswald (Höhenwald)*: Mildbraed, 1914, p. 623. *Temperate Rain Forest*: Shantz and Marbut, 1923, p. 32. *Mountain Forest*: Chipp (in Tansley and Chipp, 1926, p. 208). *Subtropischer Ge-*

birgswald: Mildbraed, 1914, p. 659. *Subtropical Evergreen Forest*: John Phillips (in this JOURN. **18**, 1930, p. 225). (In each case it is the forest below the Bamboo Zone which is represented in this community.)

This type of forest is intermediate between the Tropical Rain Forest and the Higher Temperate Rain Forest and occurs in regions where the altitude is too high for the former and the rainfall and humidity too low for the latter. The trees generally are not so large as those in the Tropical Rain Forest (*Deutsch-Ostafrikas Regenwälder*, Engler, 1910, p. 290) found at lower altitudes of from 3000 to 5000 ft., the average being about 30–40 ft. high, and from 1 to 2 ft. in diameter. They are generally not suitable for exploitation for timber. The dominant trees are rather widely spaced with an abundance of smaller trees, bushes and shrubby growth between. Epiphytes such as algae, ferns and orchids are present on the trees in the moister portions but are not so frequent as is the case in the Higher Temperate Rain Forest.

This Subtropical Forest is the natural climax in valleys, alongside streams and on the lower slopes of hills where the soil is generally deeper and more fertile. In the area traversed, however, this type of vegetation has suffered much from felling and burning to make way for the cultivated crops of the large native population resident in this zone. The largest forest areas which remain lie chiefly in the valleys running in a north-westerly direction to the west of Lake Bunyoni and on towards the Congo Forest Belt.

Of the species collected or noted in this forest, many of them are not confined to this zone, but extend either into the one below or the one above, but they differ from them in their usually less luxuriant growth. The following lists are from my own personal observations and are by no means exhaustive.

Dominant trees.

Albizzia spp. (Legum.), including *A. Sassa* Macbride, tall trees with spreading crowns of dark green fern-like foliage and producing a profusion of bright pink or purple and white flowers. *Macaranga kilimandscharica* Pax., *Croton macrostachys* Hochst., and *Neoboutonia macrocalyx* Pax., all moderately tall Euphorbiaceous trees with large palmately veined leaves and greenish or yellowish unattractive flowers. *Ekebergia Ruepelliana* A. Rich. (Meliac.), a tall tree with large pinnate leaves and long racemes of greyish white flowers. *Bersama Volkensii* Gurke (Melianth.), a much similar tree but differing in the flowers and capsular fruit. *Lannea Schimperi* Engl. (Anacard.), a tree with showy purple-coloured young pinnate leaves, inconspicuous flowers, and small mango-shaped fruits. *Spathodea nilotica* Seem, with splendid large bright scarlet tulip-shaped flowers and *Markhamia platycalyx* Sprague with smaller and less decorative yellow ones, both Bignoniaceous trees with large pinnate leaves. *Alangium begoniifolium* Harms. sub-spec. *A. eubegoniifolium* Wangerin, a spreading tree with unequal-sided simple leaves and bright yellow flowers.

Smaller trees.

Erythrina tomentosa R. Br. (Legum.), a widely distributed thorny tree with handsome bright scarlet flowers. *Ficus* spp., both small and large leaved forms. *Myrianthus arboreus* P. Beauv. (Morac.), a tree with digitate leaflets, resembling those of the horse-chestnut, and large edible cone-shaped fruits which turn yellow when ripe. *Dracaena fragrans* Gawl. (Liliac.), a large tree-like species with numerous upright and branched stems each of which is surmounted by bunches of long sword-shaped leaves and large much-branched panicles of sweet-scented white flowers.

Shrubby trees and bushes.

Abutilon spp. (Malvac.), 5–6 ft. high with large yellow flowers. *Pavonia Schimperiana* Hochst. var. *tomentosa* (Malvac.), a large spreading shrub with decorative red and purple flowers. *Dalbergia lactea* Vatke (Legum.), a small tree with pinnate leaves and lilac-purple flowers. *Cassia didymobotrya* Fresen (Legum.), a shrub or small tree with large terminal racemes of deep yellow flowers. *Indigofera arrecta* Hochst. (Legum.), the wild indigo plant with racemes of small red flowers. *Vernonia* spp. (Compos.), varying from 5 to 10 ft. high with flowers ranging from greyish white to purple. *Galiniera coffeioides* Del. (Rubiac.) a shrubby tree with sweet-scented white flowers and red fruits much resembling Robusta Coffee, especially frequent near Muko on Lake Bunyoni. *Hymenodictyon Kurria* Hochst. (Rubiac.), a small tree with leaves which turn red and purple shades with age. *Solanum* spp., shrubs from 3 to 6 ft. or more high, with greyish white or pale blue flowers and red and yellow fruits, often with prickly stems. *Acanthus pubescens* Engl., shrub from 5 to 10 ft. high with large spiny leaves and purple flowers. *Brillantaisia Mahonii* C. B. Clarke and *Barleria ventricosa* Nees, Acanthaceous shrubs from 3 to 6 ft. high with decorative blue flowers. *Clerodendron Johnstonii* Oliv. (Verben.), a sweet-scented white-flowered liane or small tree. *Lantana salviifolia* Jacq. (Labiate.), a widespread shrub 3 to 6 ft. high with purple flowers. *Coleus barbatus* Benth. (Labiate.), a somewhat fleshy leaved shrub 5 to 8 ft. high with handsome deep blue flowers. Also occasional clumps of the wild banana, *Musa Ensete* Gmel., and the arborescent *Lobelia Gibberoa* Hemsl.

Sub-shrubs and herbs.

Spiny stemmed *Rubus* spp. (Rosac.); red-flowered *Desmodium Scalpe* DC. (Legum.); yellow-flowered *Senecio, Coreopsis, Cineraria* (Compos.) and *Celsia* (Scroph.); white-flowered *Pentas longiflora* Oliver (Rubiac.), red-flowered *P. carnea* Benth., and *P. zanzibarica* Vatke with deep blood-red flowers. Still lower the ground is covered with the Forget-me-not blue of *Cynoglossum amplifolium* Steud. (Borag.) and *C. lanceolata* Forsk.; varying shades of red and pink of *Impatiens* spp.; yellow-flowered species of *Ranunculus* and *Brassica*; the fern-leaved *Thalictrum rhynchocarpum* Dill. & Rich. (Ranunc.); ferns such as

Adiantum, Asplenium and *Polypodium*; and shade-loving grasses such as *Panicum adenophorum* K. Schum., *P. Hochstetteri* Steud., *Digitaria abyssinica* Stapf, *Pennisetum trachyphyllum* Pilger, and *Setaria orthosticha* K. Schum.

(b) Subtropical Bush.

Synonymy. Part of the *Gebirgsbuschsteppe*: Engler, 1910, pp. 327, 963. In *Subtropische Buschregion*: Engler, 1910, p. 931. *Die Adlerfarn-Formation*: Mildbraed, 1914, p. 621. *The Protea-Other Species community*: John Phillips, in this JOURN. **18**, 1930, p. 223.

This type of vegetation generally covers the summit and higher slopes of the hills up to about 7000 or 7500 ft. altitude, but is also found on their lower slopes in some types of heavy clay soils which are subject to extremes of wet and cold in the rainy season, and of drought in the dry season owing to the soil cracking and drying out quickly. It is a sub-climax which would develop to Subtropical Forest were the soil conditions more favourable and fires excluded. At present this community is fire-swept in exceptionally dry weather and is the one which most nearly approaches the "Hyparrhenia-Themeda Fire-swept Savannah" of lower altitudes. The chief characteristics are the comparatively few scattered small trees between which the ground is densely crowded with shrubby plants and bushes 6–12 ft. high, mingled with which is a conspicuous undergrowth of the "Bracken Fern," *Pteridium aquilinum* Kuhn, either growing through the bushes or occasionally forming almost pure stands. Tall reed-like grasses are not infrequent near the edges of the bushes or in clearings where they have established themselves. A list of the most frequent species is given below.

Dominant trees.

Nuxia congesta R. Br., a medium-sized Loganiaceous tree with clusters of white sweet-scented flowers. *Bersama abyssinica* Fresen, with pinnate leaves and greyish white flowers like those of *B. Volkensii* Gurke, but much dwarfer and less vigorous in growth. *Erythrina tomentosa* R. Br., already referred to, *Ficus* spp. and *Bridelia* sp., a rather bushy tree with simple leaves and greenish yellowish flowers belonging to Euphorbiaceae. *Dalbergia lactea* Vatke is also found in this community.

Bushes and woody shrubs.

Dodonaea viscosa Lam., a Sapindaceous shrub or small tree having simple leaves and inconspicuous flowers followed by decorative purplish winged fruits. *Philippia benguelensis* Alm. and Th. Fr. jr., an Ericaceous shrub 3–6 ft. high with heather-like flowers and foliage. (This shrub, or an allied species, is frequently referred to by earlier writers under *Ericinella Mannii* Hook., which does not extend so far east but is mainly a West African species.) *Smithia aeschynomenoides* Welw., a Papilionaceous shrub 3–10 ft. high with pale blue flowers which together with the stems and fruits are covered with viscid oil

glands giving off a peculiar smell. *Polygala Elliotii* Chodat, a shrub 2–4 ft. high with handsome flowers of shades of light and deep purple. Shrubby species of *Vernonia* and *Pycnostachys* with blue and white flowers are also frequent.

Dominant grasses.

The most frequent tall reed-like species from 4 to 6 ft. or more high are *Hyparrhenia cymbaria* Stapf and *H. diplandra* Stapf with large panicles which are very showy on account of the conspicuous reddish brown spatheoles from which each raceme pair of spikelets arises; *Cymbopogon afronardus* Stapf which has glaucous green slightly aromatic leaves; and *Digitaria uniglumis* var. *major* Stapf, whose stout culms are surmounted by much-branched dark bluish purple panicles. Species with more slender culms are *Melinis minutiflora* P. Beauv. with spreading viscous glandular leaves, which is known as "Molasses Grass," and the strongly tufted tough-leaved *Eragrostis lasiantha* Stapf, a species which in general appearance agrees with that of *Eragrostis olivacea* K. Sch., so often referred to by earlier authors as occurring on East African mountains.

(c) *Subtropical Evergreen Scrub.*

Synonymy. Gebirgsbusch: Engler, 1910, pp. 327, 962. Included in the *Subtropische Buschregion*: Engler, 1910, p. 931. *Subtropical Evergreen Scrub*: John Phillips (in this JOURN. 1930, p. 223).

This formation is a feature of the rocky lava plains round about Chahafi and the foot-hills on the eastern and north-eastern side of Mount Muhavura where the lava rocks are either exposed or covered with only a very shallow layer of soil. In order to grow their crops in this locality, the natives frequently have to dig out the large clinker-like rocks and pile them in heaps in various parts of the plots. For the most part the vegetation consists of stunted forms of the more widely distributed and adaptable species of the trees and shrubs already mentioned under (a) and (b). All show a marked xeromorphic adaptation to enable them to succeed in the prevailing shallow, rocky soil and to withstand the strong winds which sweep across the plains between the Mufumbiro Mountains and the Behungi Range. Some achieve this by reduced and stunted growth, others by an increased hairiness or thicker and more leathery cuticle of the leaves, while many of them are protected by spines or thorns against browsing animals. Some of the latter species have been preserved or planted to form hedges near habitations or around cattle kraals in the more populous areas, which are otherwise bare of trees or bushes. These hedges provide some shelter from storms and also a protection against wild animals. The density of the scrub varies in proportion to the depth of soil overlying the lava rocks, being almost impenetrable where there is a good layer of soil, but more generally the woody plants are widely spaced and the intervening area is filled with a mixture of grasses, succulents, bulbous and tuberous rooted plants. The most frequent species noted are listed below.

Stunted or small trees.

Erythrina tomentosa, Croton macrostachys, Bridelia sp., candelabra-shaped arborescent *Euphorbia* sp., *Ficus* spp., *Grewia* sp. (Tiliac.) and *Gymnosporia senegalensis* Loes (Celastrac.), a small tree with small greenish white flowers and leathery simple leaves almost like phyllodes in appearance.

Bushes and shrubs.

Species of *Rhus, Capparis* and *Carissa*, the two latter usually with spiny stems. *Pavonia Schimperiana* var. *tomentosa, Vernonia* spp., *Solanum aculeastrum* Dun., *Coleus barbatus* and *Asparagus* spp.

Succulent plants.

Species of *Sansevieria, Aloe* and *Kalanchoe. Phytolacca dodecandra* L'Herit., a very variable and widespread species which has long racemes of tiny greenish white flowers followed by red, soapy berries. *Rumex abyssinicus* var. *angustisectus* Engl., which has large terminal panicles of red and yellow flowers, is very common here, and is also met with in other parts of South Kigezi.

Hedge plants around habitations.

Erythrina tomentosa, Ficus spp., *Solanum aculeastrum* Dun., *Coleus barbatus.* Growing among these are frequently *Rumex abyssinicus* var. *angustisectus, Indigofera arrecta* and *Senecio Petitianus* A. Rich., a succulent-stemmed climbing species.

(d) Subtropical Moist Meadowlands.

Synonymy. Das feuchte Hochweideland: Engler, 1910, pp. 332, 953.

This community is found mainly on the richer alluvial lands of the plains and valleys and has been formed after the Subtropical Forest described under (*a*) has been cut down and burnt. The land has then been used for the cultivation of food crops for a few years, following which the old cultivations have been abandoned and have been invaded by low-growing grasses possessing strong perennial rhizomes which soon formed grazing lands frequented by stock and thus effectually prevented any return to the natural forest climax. This type of vegetation is green throughout most of the year and differs from savannah pasture in not being fire-swept. Tufted savannah grasses are few, but if present they assume a more spreading and procumbent habit than they do on fire-swept pastures. The dominant and characteristic grass is *Pennisetum clandestinum* Hochst. (Kikuyu Grass), which is now known to be one of the most nutritious grasses in Central and East Africa. This, together with associated grasses listed below, makes an excellent springy short deep-green turf, usually varying from 3 to 6 in. high, which provides very good feed for all kinds of stock. These meadows are exactly like English meadows in appearance and differ only in the species which compose them.

Dominant and typical grass.

Pennisetum clandestinum Hochst.

Co-dominant grasses.

Andropogon abyssinicus R. Br., with soft leaves, *Pennisetum Snowdenii* C. E. Hubbard and *Sporobolus indicus* R. Br. with rather tougher foliage, are three grasses characteristic of this community. Those having a wider altitudinal range and commonly found in the next lowest altitudinal zone are *Digitaria scalarum* Chiov., *Cynodon plectostachyus* Pilger, and *Eragrostis tenuifolia* Hochst. The two former have soft thin leaves and the latter rather tough ones, though all are useful grasses. *Digitaria scalarum*, however, is a most troublesome weed in cultivated lands, as the rhizomes are difficult to eradicate. *Cynodon Dactylon* Pers. and *C. transvaalensis* Burtt-Davy are two exotics formerly introduced for lawns and Rest-house compounds which are now naturalised and easily maintaining themselves or even becoming dominant grasses near roads, paths and habitations.

Other grasses.

Exotheca abyssinica Anders. and *Setaria sphacelata* Stapf and Hubbard (better known as *Setaria aurea* Hochst.), two widely distributed grasses which seem capable of flourishing under very variable conditions, are fairly frequent. *Brachiaria decumbens* Stapf, *Setaria pallidifusca* Stapf and Hubbard, *Arthraxon Quartinianus* Nash., and *Rhynchelytrum roseum* Stapf and Hubbard, are all useful widely distributed grasses, which occur here and there but may almost be regarded as intruders. Owing to close grazing none of the species mentioned exceeds 1 ft. high, except the few flowering culms which escape being eaten off when young.

Plants other than grasses.

These are almost hidden among the grasses, being mainly from 3 to 9 in. high, and include *Oxalis corniculata* L., *Lobelia stellarioides* Benth. and Hook., *Trifolium polystachyum* Fres., *Vicia sativa* Linn., *Veronica abyssinica* Hook. f. (Scroph.), *Alchemilla mukuluensis* De Wild (Rosac.), *Linum gallicum* L. var. *abyssinicum* Planch., and *Geranium simense* Hochst.

(e) *Subtropical Drier Pasturelands.*

Synonymy. Trockeneres Weideland: Engler, 1910, p. 331. *Trockenes Gebirgsweideland oder Hochgebirgssteppe*: Engler, 1910, p. 964. *Mountain Grassland*: Shantz and Marbut, 1923, p. 67. Chipp (in Tansley and Chipp, 1926, p. 212).

These pastures have arisen owing to the burning and destruction of the Subtropical Bush and Bracken Fern Community, described under (*b*), in much the same way as the moister meadowlands arose following the destruction of the Subtropical Forest. This type of vegetation is found mainly on the higher

slopes of hills or, if lower in the valleys, where heavy clay lands are prevalent and the soils are less mature and not so fertile. The grasses which compose these pastures are essentially savannah species, often found in the next lower vegetational zone, and are kept dwarf owing to frequent grazing. They are occasionally fire-swept in the drier districts. They are generally not quite so nutritious as those of the moist meadowlands, being rather more woody in the flowering stage, but are more resistant to drought. The flowering culms range mostly from 3 to 5 ft. in height when mature, but are often kept much shorter when closely grazed.

Dominant species.

Hyparrhenia spp. varying with the locality and including *H. filipendula* var. *pilosa* Stapf, *H. Lecomtei* (Franch.) Stapf, *H. collina* Stapf, and a variety of *H. cymbaria* Stapf, which is much dwarfer and weaker growing than the typical form. *Exotheca abyssinica* Anderss. and *Setaria sphacelata* Stapf and Hubbard (better known as *Setaria aurea* Hochst.). Practically all of the same height (3–5 ft.).

Frequent dwarfer species.

Eragrostis chalcantha Trin., *E. lasiantha* Stapf, a densely tufted rather tough grass, and *Eragrostis* sp. near *E. Chapelieri* Nees (No. 1447), a rather stiff wiry grass.

Less frequent.

Themeda triandra Forsk. var. *hispida* Stapf, *Microchloa indica* P. Beauv., and *Sporobolus* sp. (No. 1498).

(f) Subtropical Swamp and Aquatic Vegetation.

Synonymy. Formation der gemischten Sumpfpflanzen in höheren Regionen: Engler, 1910, p. 947. *Die Papyrussümpfe*: Mildbraed, 1914, p. 615. *Swamp and Aquatic Vegetation*: Chipp (in Tansley and Chipp, 1926, p. 213).

The vegetation found in and near the edges of the many lakes and streams, at an altitude mostly from 5800 to 6500 ft., is much the same as that found under similar wet or swampy conditions at lower altitudes. The wild date palm (*Phoenix reclinata* Jacq.), however, which is so frequent in or near swamps and streams of less elevation, is very rarely seen and was observed only on the islands in Lake Mutanda (5877 ft. altitude). It seems probable that the altitudinal range of this palm does not exceed 6000 ft. in Uganda.

Dominant reed–like species.

Cyperus Papyrus L., *Cladium jamaicense* Crantz (Cyperac.), *Typha australis* Schum. and Thonn., and *Phragmites vulgaris* Crep. (Gramin.). These range from 5 to 15 ft. in height. They may be found either as pure dominant stands, or more frequently as a mixed association, either in shallow water or in swampy land subject to flooding.

Floating species.

In fairly deep water the dominants are water-lilies of the *Nymphaea stellata* Willd. section, with large decorative flowers of varying shades of blue and purple, and *Potamogeton fluitans* Roth., which has small spikes of inconspicuous greenish flowers.

Dwarf herbaceous species.

These form separate communities in areas where the dominant species have not yet established themselves sufficiently to overshadow them. They are mainly from 2 to 5 ft. high, consisting principally of species of *Cyperus*, *Polygonum* and Ferns, especially *Asplenium* and *Polypodium*. A creeping *Crassula* near *C. pentandra* Schoenl. (No. 1506) is also frequent near the water's edge in land kept free from high growth by grazing or cultivation.

Dominant grasses.

Miscanthidium violaceum (K. Schum.) Robyns, *Echinochloa Crus-Pavonis* Stapf and *Pennisetum trachyphyllum* Pilger. When mature these are rather reed-like grasses 4 to 6 ft. or more high. The two latter provide good fodder, while the *Miscanthidium* has long much-branched decorative panicles of reddish purple spikelets.

Arborescent and woody species.

The most frequent near water or in swampy lands are: *Mitragyne macrophylla* Hiern. (Rubiac.), a small tree which has conspicuous reddish stipules to the leaves and bears clusters of white flowers; *Syzygium cordatum* Hochst. (Myrtac.) and *Conopharyngia* sp. (Apocyn.), both trees with simple leaves and white flowers; and shrubby species of *Aeschynomene* (Legum.) which have yellow flowers. *Maesa lanceolata* Forsk. (Myrsin.) and *Erythrina tomentosa* R. Br. are also frequent, the latter seeming capable of succeeding under most variable conditions ranging between extremes of moisture and drought. The arborescent *Lobelia Gibberoa* Hemsl. is abundant in some areas, particularly near Kumba, where it is associated with the *Syzygium* and *Conopharyngia* already mentioned. *Phoenix reclinata* Jacq. is rare.

(2) THE TEMPERATE ZONE.

This covers that part of Engler's *Höhenwaldregion* which lies immediately below the same author's *Subalpine and Alpine Region* and ranges between the approximate altitudes of 7500–10,000 ft. In Kigezi it is comparatively small in extent and is confined to two localities, one being situated on and between the two high mountain ridges which separate Lake Bunyoni from the Bufumbira plains, and the other on the Mufumbiro Range itself.

The climate of this zone is much cooler and more temperate than that of the Subtropical Zone. There are no records available with regard to the temperature and rainfall, but there is evidence in the vegetation of much lower

temperatures and a higher humidity than is met with in the zone below. The rainfall is approximately the same, but mountain mists are more frequent and dense so that there is much less sunlight. As an indication of the climate it should be noted that the ordinary tropical crops such as maize, sorghum, millet, sweet potatoes, yams, bananas, etc., cannot be successfully grown in this zone. Peas (*Pisum sativum* L.) can be grown in parts, but natives very rarely cultivate any crops at this altitude though they herd their stock up to 8000 or 9000 ft.

The hollow-stemmed bamboo (*Arundinaria alpina* K. Schum.) is one of the chief characteristic features of this zone, the temperate nature of which is indicated by the appearance here and there of occasional clumps of *Erica arborea* L. and *Hypericum lanceolatum* Lam., and representatives of temperate genera of grasses such as *Bromus, Festuca, Calamagrostis* and *Avenastrum*. Mosses and lichens are very frequent on trees and also on the ground. The most characteristic tree is *Hagenia abyssinica* Gmel. Whereas *Juniperus procera* Hochst. and *Podocarpus* spp. do not occur in Kigezi, they are found in this type of plant formation on many other mountains of East Tropical Africa. There are a number of communities in this zone, the most important of which are given below.

(a) Bamboo and Temperate Forest.

Synonymy. Bambuswald und Höhenwald oder Nebelwald: Engler, 1910, pp. 952, 953. *Der Bambusbestand und eigentliche Höhenwald*: Engler, 1910, p. 364. *Bambusbestände*: Mildbraed, 1914, pp. 643, 646. *Laubwald mit Bambusgrasern; Bambusmischwald*: Mildbraed, 1914, pp. 659, 660.

This is the climax community in this zone wherever the soil is sufficiently deep and mature. It may consist of a mixed association of bamboos and forest trees; the bamboos may form pure stands, or they may be absent from some areas. This would appear to be mainly due to differences in the composition of the soils. The bamboos thrive best in deep soils rich in humus which allow their thick rhizomes to spread freely. The Temperate Forest trees can thrive where the soil conditions are not quite so good but of sufficient depth. In both cases there is a closed canopy above.

Dominant.

Arundinaria alpina K. Schum., a hollow-stemmed bamboo, reaching 40 ft. or more in height under favourable conditions, which is widely distributed on East African mountains between 7500 and 10,000 ft. altitude. It is almost absent from Mount Muhavura, as the lava rocks are so near the surface on that mountain, but occurs on the adjacent slopes of Mgahinga and Sabinio where the soil is deeper. *Hagenia abyssinica* Gmel., a large tree belonging to the Rosaceae, which has long pinnate leaves and large grape-like pendant branches of papery pinkish flowers. *Dombeya leucoderma* K. Schum., a Sterculiaceous

tree 20–40 ft. high, with large white flowers. *Hypericum lanceolatum* Lam., a large shrub or small tree with large handsome yellow flowers.

Frequent.

Nuxia congesta R. Br. and species of *Croton, Macaranga, Neobutonia* and *Lannea* occur here and there in some parts of the Bamboo Forest up to 8000 or 9000 ft. altitude. Smaller trees and woody shrubs are *Rhamnus prinoides* L'Herit., a small tree with yellowish green flowers; *Dracaena reflexa* Lam. var. *nitens* Baker; *Pycnostachys* sp. near *P. Volkensii* Gurke (No. 1582), a small shrubby Labiate tree with decorative bluish purple flowers; *Myrica arborea* Hutch., a small tree with inconspicuous greenish flowers dotted with tiny yellow sweet-scented oil glands; *Agauria salicifolia* Hook., a low Ericaceous tree with small greenish flowers. *Erica arborea* L., with its pretty purple and white flowers, is also frequent, but is more characteristic of the Heath or Subalpine Zone.

(b) Temperate Bush.

Synonymy. Hochgebirgsbusch zwischen und über den Höhenwäldern: Engler, 1910, p. 953.

Where the rocks are too near the surface and the soil too shallow to support the Bamboo and Temperate Forest, the vegetation is reduced to shrubby trees or bushes scattered here and there, with the spaces between filled in with sub-shrubs, herbs, grasses, or bulbous plants. A similar type of vegetation is found near the edges of the forest and in open clearings.

Dominant shrubby trees.

Myrica arborea Hutch., *Agauria salicifolia* Hook., *Erica arborea* L., *Rhamnus prinoides* L'Herit., *Pycnostachys* sp.

Frequent shrubs.

Hibiscus diversifolius Jacq., with thorny stems and decorative dark-purple flowers. *Sparmannia abyssinica* Hochst. (Tiliac.), flowers pink. *Crotalaria agatiflora* Schweinf. (Legum.), with large yellow flowers. *Tephrosia atro-violacea* Bak. f. (Legum.), with blue flowers. *Cluytia abyssinica* Jaub. and Spach. (Euphorb.).

Herbaceous perennials.

Kniphofia Thomsoni Baker (Liliac.), with tall spikes of decorative red and yellow flowers; *Gladiolus Quartinianus* A. Rich. (Iridac.), with large handsome spikes of salmon-pink flowers; *Aristea alata* Baker (Iridac.), a smaller plant with blue flowers; and *Satyrium sacculatum* Rolfe, a terrestrial orchid with bright red flowers, are the most frequent of tuberous rooted species. Common suffruticose species include the decorative, yellow-flowered *Cineraria Kilimandscharica* Engl. (Compos.); the scandent, prickly stemmed *Dipsacus pinnatifidus* Linn., with spherical heads of white flowers and fruits resembling the

common "Teasel"; the handsome yellow-flowered *Celsia densifolia* Hook. f. (Scroph.); the aromatic-leaved, blue-flowered *Calamintha simensis* Benth. (Labiate) and *Salvia nilotica* Vahl (Labiate); and a *Justicia* sp. (No. 1587) near *J. leptocarpa* Lindau (Acanthac.), which has small white flowers with reddish purple stripes. Still smaller herbs common among the bushes are *Parochetus communis* Buch. Ham. (Legum.) and *Viola abyssinica* Steud. with blue flowers, the tiny white-flowered *Cerastium africanum* Oliv. (Caryoph.), and the scandent *Lathyrus intricatus* Baker (Legum.) with yellow flowers.

(c) *Temperate Swamp and Bog Vegetation.*

Synonymy. Part of the *Formation der gemischten Sumpfpflanzen in höheren Regionen*: Engler, 1910, p. 948 (near the Subalpine Region).

In very wet or boggy lands in the Temperate Zone peat-loving plants form a distinct community. The most noteworthy example in Kigezi is that formed in the peaty swamp-like depression between the Behungi Ridge and the one nearer to Lake Bunyoni. The dominants are species of shrubby *Helichrysum*, arborescent *Lobelia*, tall *Kniphofia*, together with species of *Eriocaulon*, *Ranunculus*, *Cynoglossum* and *Plantago*. Only a few representatives are listed below, many not being in flower at the time of my visit.

Species noted.

Helichrysum elegantissimum Less. (Compos.), a small shrub with decorative white flowers. *H. declinatum* Less., a procumbent species with small white flowers. *Lobelia Mildbraedii* Engl., a tall arborescent species with spikes of blue flowers, which latter are almost hidden by the green bracts. *Kniphofia zombensis* Baker, with tall spikes of handsome red and yellow flowers like *K. Thomsoni* Baker, *Eriocaulon Schimperi* Koernicke, with white flowers. A densely tufted grass *Pennisetum* sp. (No. 1454) near *P. Snowdenii* C. E. Hubbard, which has purplish spike-like racemes. *Ranunculus pinnatus* Poir, with yellow flowers. *Cynoglossum amplifolium* Steud. *Plantago palmata* Hook. f.

(d) *Temperate Grasslands.*

Synonymy. Bergwiesen: Mildbraed, 1914, p. 646.

Where neither forest nor bush have been able to establish themselves owing to the presence of rocks near the surface, or have been cut down for house-building and fuel and unable to re-establish themselves on account of browsing animals, grasslands often cover a considerable area. The grasses frequenting these open lands and clearings in the forest have more in common with those of more temperate countries than those dealt with in the Subtropical Zone. They are also not fire-swept and are not kept so closely grazed, hence they do not form short turf but are generally tufted species 1 ft. or more high with the fibrous remains of the previous seasons growth clustered around the base. A few of the subtropical moist meadow grasses form the lower ground covering

between these tufts up to 8000 ft. altitude. Ground mosses are also frequent, especially *Campylopus Hoehnelii* (C.M.) Par.

Dominant tufted species in open lands.

Calamagrostis epigeios (L.) Roth., a strongly tufted leafy grass 2–3 ft. high. *Avenastrum* sp. (Nos. 1473, 1608), probably *A. lacnanthum* (Hochst.) Pilger and *Festuca* sp. (No. 1606) near *F. gigantea* (L.) Vill., both fairly leafy grasses of the same height. A strong-growing form of *Sporobolus indicus* R. Br., a rather tough but fairly leafy grass. *Hyparrhenia mobukensis* Chiov., a slender-culmed grass covering a large area on Mount Muhavura and kept low by fairly frequent grazing by stock. Two coarser strongly tufted grasses are *Andropogon amethystinus* Steud., especially prevalent at higher altitudes, and *Pennisetum* sp. (No. 1454) near *P. Snowdenii* C. E. Hubbard. For fodder these two grasses would need frequent cutting to ensure young growth. Less leafy and bulky, though softer grasses are *Poa perlaxa* Pilger, *P. leptoclada* Hochst., *Agrostis Schimperiana* Hochst. and *Festuca* sp. (No. 1459) near *F. Camusiana* St Yves, which vary from 1 to 3 or 4 ft. high. A less frequent strongly tufted grass is *Eleusine Jaegeri* Pilger.

Species frequent near bushes and trees.

Bromus runssoroensis K. Schum., a strong-growing leafy grass 2–3 ft. high. *Brachypodium flexum* Nees, *Ehrharta erecta* Lam. var. *abyssinica* Pilger, *Agrostis* sp. (No. 1488) and a *Panicum* sp. (No. 1491) near *P. calvum* Stapf, all of which are fairly leafy grasses from 1 to 3 ft. high. Two weak-culmed grasses sometimes trailing over bushes are *Hyparrhenia mobukensis* Chiov. and *Acritochaete Volkensii* Pilger.

Suffruticose herbs among the grasses.

Crambe hispanica L. (Crucif.) with white flowers. *Helichrysum globosum* Sch. Bip., *H. fruticosum* Vatke, *Conyza* sp. (No. 1538) near *C. Gouanii* Willd., *Senecio ruwenzoriensis* S. Moore, and *S. Hochstetteri* Sch. Bip., all Compositae from 1 to 3 ft. high and having yellow flowers. A frequent aromatic Labiate shrub, 1–2 ft. high, with blue flowers, is *Micromeria biflora* Benth.

Small herbs almost hidden in the grasses.

Cerastium viscosum L. (Caryoph.) and *Cardamine hirsuta* L. (Crucif.), both with small white flowers. *Galium Aparine* L. (Rubiac.) and *Galium* sp. (No. 1529), with tiny greenish yellow flowers. *Mariscus* sp. (No. 1532, Cyperac.).

II. THE EAST AFRICAN MOUNTAIN SUBALPINE AND ALPINE FORMATION.

Synonymy. Subalpine and alpine Formationen Ostafrikas: Engler, 1910, p. 341.

This formation occurs above the limit of the Temperate Forest and extends from approximately 10,000 ft. up to the uppermost limit of plant growth. As

there is a considerable difference in the vegetation of the lower and upper part of this formation, especially as regards the height and luxuriance of growth, I think it best to divide it into two zones (1) Subalpine and (2) Alpine.

(1) SUBALPINE ZONE.

Synonymy. Subalpine Formation Ostafrikas: Engler, 1910, pp. 341–2, includes the area up to a height of 3500 m. Part of the *Bergwiesen*: Volkens, 1897, p. 306. *Formation der Ericaceen oder Subalpine Sträucher* and *Die Senecio-Formation*: Mildbraed, 1914, pp. 639, 644–5, 647–8. Stuhlmann's *Region der Formation der baumartigen Senecionen, Schaftlobelien und Helichrysumsträucher*: Mildbraed, 1914, p. 664. *Hochmoor mit Ericawald* (3200–3800 m.), *mit Lobelien und Senecien*: Stuhlmann with Emin Pascha, 1894, p. 300.

This zone extends from approximately 10,000 to 12,000 ft. altitude on the Mufumbiro Range of South Kigezi. The climate is much colder than that of the Temperate Zone and night frosts are not infrequent. There is very little bright sunlight and the vegetation is frequently enshrouded in dense mists or in their absence exposed to strong cold winds or icy-cold rains. It is marked by the cessation of bamboos and trees, the increasing number of shrubs of *Erica arborea* sometimes associated with *Philippia Johnstonii* Engl. (Ericaceae) and arborescent Lobelias which here include *L. Wollastonii* Bak. f. together with Tree Senecios, *S. Erici-Rosenii* R. E. and Th. C. E. Fries being the dominant species. Areas not occupied by such shrubby species as the above are covered mainly with a mixture of mosses, grasses and species of *Helichrysum*. This zone may be divided into several smaller communities but as many species were not in season at the time of my visit the lists are by no means complete.

(a) *Arborescent* Senecio *and* Lobelia *Community.*

Synonymy. Oberste Schopfbaumformation: Engler, 1910, p. 965. *Senecio-Formation*: Mildbraed, pp. 644–5, 648. *Baumformige Senecien und Lobelien*: Stuhlmann, 1894, p. 300.

The arborescent Senecios and Lobelias are often grouped together in a mixed association forming the climax community in valleys and hollows where the soil is deeper and richer. The former are often so close as to form a covered canopy above and in such places reach up to 20 or even 30 ft. in height, so that they form a miniature forest, with their tree-like branches festooned with thick mosses. In exposed places and shallow soils they are more scattered and more dwarf. Occasional trees of *Myrica arborea*, *Agauria salicifolia* and *Hagenia abyssinica* are found in this community at lower altitudes up to about 11,000 ft.

Dominant species.

Senecio Erici-Rosenii R. E. and Th. C. E. Fries (Compos.), from 12 to 20 ft., rarely 30 ft. high, flowers yellow on large compound racemes 1–2 ft. long. *Lobelia Wollastonii* Bak. f. with long flowering spikes which reach from 5 to 15 ft. high.

Other species.

Helichrysum Newii O. and H., a low shrub up to 1½ ft. high, outer florets white, mostly curved over and hiding the yellow central florets. *Peucedanum runssoricum* Engl., an Umbelliferous plant 3–4 ft. high with greenish yellow flowers. *Senecio subsessilis* Sch. Bip., 3–4 ft. high, flowers yellow, in heads about 1½ in. across.

(b) Subalpine Bush.

Synonymy. Oberste Buschgeholze steinigen Bodens: Engler, 1910, p. 965. *Ericaceen oder subalpine Sträucher*: Mildbraed, 1914, pp. 644, 647, 649.

On exposed slopes, where there is only a shallow layer of soil and the rocks often appear above the surface, the vegetation is reduced to low shrubs and bushes, mainly of *Erica* and *Philippia*, with stunted trees of *Myrica arborea* and *Agauria salicifolia* or occasionally *Hagenia abyssinica* at the lower altitudes. The ground in between the bushes is covered with grasses, mosses and herbaceous plants.

Dominant species.

Erica arborea L., *Philippia* spp., *Helichrysum* spp.

(c) Subalpine Meadows and Moorland.

Synonymy. Oberste alpine Bergwiesen: Engler, 1910, p. 965. *Hochmoor*: Stuhlmann, 1894, p. 300. *Die Heidemoore*: Mildbraed, p. 627. *Bergwiesen* (partly): Volkens, 1897, p. 306. *Alpine Meadows* (partly): Shantz and Marbut, 1923, p. 67.

This occupies the areas where the arborescent and bush species have not yet been able to establish themselves owing to unfavourable substratum or exposure. On Mount Muhavura *Andropogon amethystinus* Steud. is the dominant species up to about 11,000 ft. on shallow soils overlying lava rocks, many of which are exposed above the surface and entirely bare of vegetation except for a few lichens. This grass forms pure stands covering large areas, its dense tufts rising 2–3 ft. high and its rootstocks are raised from 6 to 9 in. above the general level of the ground, making walking very difficult. Above 11,000 ft. the ground covering is largely composed of thick sphagnum-like mosses which are very treacherous to walk upon, as sometimes one's foot sinks down unexpectedly into a hidden hole or crevice 1 or 2 ft. below the general surface. The few grasses which occur are closely related to European species and have either rolled or narrow leaves. Species of *Alchemilla* form a carpet of silvery leaves covering large stretches of ground here and there among the mosses.

Dominant species.

Grasses: *Andropogon amethystinus* Steud., *Festuca abyssinica* Hochst., with very slender, mostly rolled leaves. *Poa* sp. (No. 1480) with flat, wider, but still narrow, leaves.

Mosses: *Braunia secunda* (Hook.) Bry. eur., *Polytrichum Hoehnelii* (C.M.) Par., *P. piliferum* Schreb., and *Rhacomitrium hypnoides* (L.) Lindb. Frequent flowering plants associated with these are *Alchemilla aberdarensis* De Willd., with silvery leaves and tiny yellow flowers. *Helichrysum Newii* O. and H., a low shrub with white ray and yellow tubular florets, already mentioned.

<div align="center">(2) ALPINE ZONE.</div>

Synonymy. Alpine Formation Ostafrikas: Engler, 1910, p. 342, includes the area above 3500 m. *Oberste alpine Bergwiesen*: Engler, 1910, p. 965, the upper part only. *Die Bryophyten-Vegetation und Alpine Moore*: Mildbraed, 1914, pp. 645-6. *Trockenes Moos und Flechten mit kleinem Gestrauch und Baum-förmigen Senecien und Lobelien*: Stuhlman, 1894, p. 300. Mildbraed, 1914, pp. 657, 664-5.

This is the highest vegetational zone. On the East African mountains it extends from about 12,000 ft. up to the limit of plant growth in the region of perpetual snow and ice. The night temperature is often below freezing-point. During the short time I was in this zone on Mount Muhavura the temperature about noon varied between 40 and 50° F. The sun was obscured by mist practically the whole time, and the higher temperatures were recorded when it was least dense. Night temperatures must be considerably lower. In South Kigezi this zone is found only on Mount Muhavura, where it extends from 12,000 ft. to the summit, 13,547 ft. There is no permanent ice or snow on this mountain as it is not sufficiently high. The alpine flora is comparatively poor in species, unless my visit was at an unfavourable time. Near the summit there is a small, almost circular, crater lake, about 100 yards across, but this appeared to be quite clear of vegetation. Mosses and *Alchemilla* with a few grasses form the principal ground covering, while the arborescent *Senecio alticola* Th. Fries and *Lobelia Wollastonii* Bak. f. are the two dominant species rising above this, the latter occurring mainly up to 12,500 ft. and not reaching to the summit.

The following are the species noted:

Senecio alticola Th. Fries at lower altitudes may attain as much as 10 ft. in height, but at the summit rarely exceeds 5 ft.: the leaves are densely covered with white woolly hair, the flower heads are yellow, about 1 in. across, and the inflorescence is much branched and 1-2 ft. or more long. *Lobelia Wollastonii* Bak. f., *Alchemilla aberdarensis* De Willd., *Helichrysum Newii* O. and H., *Swertia crassiuscula* Gilg., a tiny Gentian with blue flowers. *Luzula Volkensii* Bucher. The few grasses which were noted in this zone include *Festuca abyssinica* Hochst., *Deschampsia ruwenzorensis* Chiov., *Anthoxanthum nivale* K. Schum., and a *Poa* sp. (No. 1481), the two former having rolled leaves and the two latter flat narrow ones. None of them exceeds 1 ft. in height. The mosses extending up to the summit include *Stereodon cupressiformis* (L.) Brid., and *Breutelia subgnaphalea* (C.M.) Par. Lichens were frequently encrusted on exposed rocks, but their names were not determined.
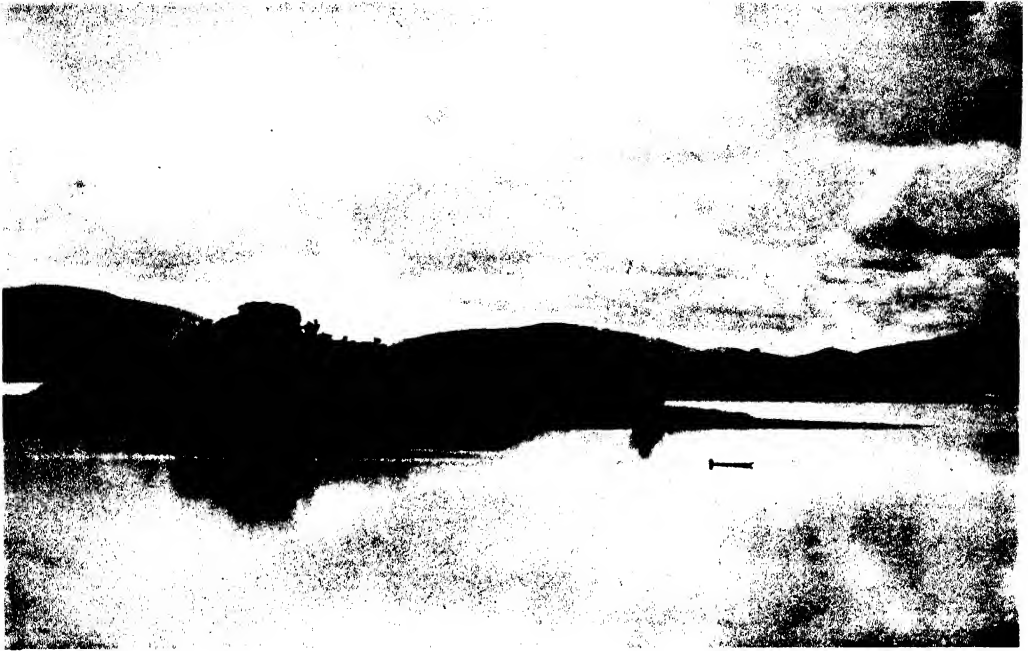
Phot. 1. Island in Lake Bunyoni, opposite Bufundi Camp. *Dracaena fragrans*, arborescent *Euphorbia* sp. and *Ficus* spp., remains of forest vegetation on hill-top of island; cultivated plots and moist meadow grazing lands below.

Phot. 2. Bufundi Camp, with rest-house, tree Euphorbias, small trees of *Markhamia platycalyx*, and *Acacia decurrens* "Black Wattle" (introduced). *Cynodon Dactylon* and *C. transvaalensis* (both naturalised), *Digitaria scalare* and *Chloris pycnothrix* form the lawn.

SNOWDEN—ALTITUDINAL ZONATION IN SOUTH KIGEZI

Phot. 5. Mt Muhavura, showing summit clear and faint track up to it. Temperate grasslands below with cattle grazing and a large

Phot. 3. Lakes Mugishu and Chahafi, E. slope of Mt Muhavura on right. Taken from Behungi Camp looking S.W. *Arundinaria alpina* in foreground. Near hills are covered with temperate grassland vegetation, used as grazing land.

SNOWDEN— ALTITUDINAL ZONATION IN SOUTH KIGEZI

During the course of the tour specimens of most of the plants cited in the text above were collected and forwarded to the Royal Botanic Gardens, Kew, for the purpose of identification. I take this opportunity of recording my appreciation of the help received from the Director and his Staff, especially the Keeper of the Herbarium and his assistants, for so kindly identifying the material, comprising over two hundred numbers, mostly distinct species, a set of which has now been deposited in the Herbarium, Kew. The numbers given in brackets refer to those specimens in cases where specific determination is not yet available. I have also to thank Dr W. B. Turrill for some helpful suggestions in reference to this paper.

SUMMARY.

1. The purpose of this article is to record the author's observations on the vegetation of South Kigezi as a contribution which may be helpful to others who may be able to make a more detailed study of the flora.

2. The locality, physiography, area traversed, soils and climate are briefly mentioned.

3. The vegetation is divided into two main formations, the Subtropical Formation and the Subalpine and Alpine Formation.

4. These two formations are each subdivided into two separate zones. The former into the Subtropical and Temperate Zones, and the latter into the Subalpine and Alpine Zones.

5. The climatic and vegetative features of each zone are briefly dealt with and the most important communities are described, lists of species with notes being given.

6. In each zone, special attention is given to meadow, pasture, and grassland communities, as these cover the largest area and are of particular economic importance.

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THE VEGETATION OF MPWAPWA, TANGANYIKA TERRITORY

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(With Plates III–VI and three Figures in Text.)

INTRODUCTION.

MPWAPWA lies about twelve miles north of Gulwe Station on the Central Line on the eastern borders of the Central Province, Tanganyika Territory and at the western foot of the Usagara Mountains.

According to German records its position is given as longitude 36° 23′ E. of Greenwich and latitude 6° 21′ S., but it is not certain if this reading applied to the German Administrative Post, now a ruin, or to the headquarters of their Veterinary Research Department, the present headquarters of the Department of Veterinary Science and Animal Husbandry for Tanganyika Territory.

TOPOGRAPHY.

Gulwe is about 2500 ft. above sea-level and one gradually ascends to about 3500 ft. at Kikombo a little to the north of Mpwapwa, where the headquarters of the Veterinary Department are situated and the main area with which this paper is concerned (see map).

Kikombo is more or less surrounded by steep-sided rocky hills, the highest of which, the Kibariani Range, to the north-east attains a height of 6100 ft. The area is intersected by a number of watercourses, only four of which contain water in their upper reaches at the end of the dry season.

On the west these hills appear to be separated from the adjoining hilly country by a very wide valley, through which the Kinyasungwi River passes in a very ill-defined channel.

GEOLOGY OF THE AREA[1].

"This mountain mass and the Usagara and Uluguru Mountains are members of the same rock formation, namely the ancient Crystalline Complex. The rocks examined were mainly biotite gneisses and injected quartz interfoliated with the gneisses. The biotite gneisses vary in composition from a soft variety

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[1] Extract from a MS. Report on Mpwapwa Water Supply by **T. B. Wade**, Senior Assistant Geologist, Tanganyika Territory, dated August 14th, 1928, in the records of the Veterinary Department.

Scale

0   ½   1   2   3   4   5   Miles

KIBARIANI

Kibariani Mission

RANGE (1700—1800 metres high)

STEILER MOUNT.

BAUN. MT.

KISSOKWE VALLEY

KLIPPEN MOUNT.

Forest

WALD MT.

MISSION STREAM

NORD MT. (Circa 1400 m.)

Vet.y Station

KIKOMBO VALLEY

NKUNDA HILL

NKUNDA STREAM

KIBARIANI STREAM

To Kissokwe

Native Village MPWAPWA

Old German Headquarters

To Gulwe

Kikombo R.

NDEGETA MT. (Circa 1400 metres)

Mission

LUGALLA PEAK (Circa 1500 metres)

To Tubugwe

MAP SHEWING
VETERINARY STATION AREA
AT
MPWAPWA

Roads
Intermittent streams
Native paths
Contour lines

29   31   33   35   37   39

UGANDA

KENYA

CONGO

Kigoma

Railway

TANGANYIKA

MPWAPWA

Gulwe

INDIAN OCEAN

BELGIAN

TERRITORY

Dar es Salaam

RHODESIA

NYASALAND

Scale

0   100   200   Miles

PORTUGUESE E. AFRICA

29   31   33   35   37   39

FIG. 1.

composed almost entirely of biotite with a little quartz and felspar to a hard more quartzose rock containing only specks of biotite. The former soft rock seems to be the water-bearing formation, and the latter with pure quartz injections provides the impervious formation to which is attributed the existence of most of the springs.

"The strike of the gneisses varies from 305 to 320° and the dip to the south-west varies from nearly vertical to 55°."

SOILS.

The soils in the area are extraordinarily variable. In colour they range from grey, almost white, through blacks, browns and yellows, to a very bright red.

On the hills and mountain slopes they are very stony, often extremely shallow, ranging through the yellows and browns and appear to contain very little humus.

On the more gentle slopes and in the valleys the greys, blacks, and reds are represented.

The greys are generally sandy and occur in the stream beds and along their banks. They contain to a certain extent small rounded stones and a little humus.

The blacks are heavy and occur as irregular bands or patches on slopes, like the reds. The former in sections contain scattered boulders and after rains appear to dry out with a certain amount of cracking. These bands of black soils may indicate the positions of old erosion channels and stream beds which have become filled up with soil washed down from the mountain slopes during past times.

The red soils range from a brownish red to a very bright red, they contain small irregular-shaped stones, are somewhat clayey and appear to be formed *in situ* and contain very little humus.

The humus content of the soils in the whole area is very low. This, no doubt, is due to the activities of white ants, as they are very abundant.

The whole area is broken by deep wet-season watercourses, and in places where the vegetation has been removed erosion channels have formed and are forming on the gentlest of slopes. In these, good soil profiles can be seen and in their lower reaches the soil appears to be very deep and of a fairly uniform colour and texture throughout.

CLIMATE.

The climate is dry; the coolest month of the year is July, the hottest February, but according to German records, November was the hottest.

The annual rainfall appears to be somewhat variable; during the period 1911–12 and 1926–8 the maximum annual rainfall was 44·70 in. in 1927 and the minimum 19·93 in. in 1928. The same applies to the monthly rainfall, but if the average is taken February with 5·7 in. is the wettest for 1911–13 and

1926–8. March for the same period runs it very close with 5·6 in. but June to October are practically rainless for an average of 6–7 years.

<div align="center">

Temperatures[1].

</div>

	1927		1928		
Month	Max. ° C.	Min. ° C.	Shade max. ° C.	Shade min. ° C.	Sun ° C.
January	32·5	14·5	34	13	71
February	34·0	13·0	35	13	71
March	32·5	15·0	31	14	72
April	30·0	14·0	29	15	70
May	28·5	14·0	30	16	65
June	28·5	13·0	28	13	65
July	26·5	12·0	27	8	62
August	28·0	11·5	28	10	67
September	29·5	11·0	31	10	70
October	31·0	12·0	34	9	66
November	33·0	12·0	32	12	66
December	33·0	15·0	32	12	68

[1] *Annual Reports: Department of Veterinary Science and Animal Husbandry, Tanganyika Territory,* 1927.

<div align="center">

Rainfall[1].

</div>

	Year							Total		Monthly averages for number of year		
Month	1910	1911	1912	1913	1926	1927	1928	mm.	in.	mm.	in.	
January	—	77·7	64·8	124·6	190·3	201·8	61·8	721·0	28·34	120·16	4·73	Six
February	—	68·1	325·6	101·0	146·6	132·8	86·2	860·3	33·87	143·38	5·64	,,
March	—	139·1	148·4	215·3	28·6	162·0	157·8	851·2	33·51	141·86	5·58	,,
April	45·7	60·0	65·4	115·9	52·6	302·4	31·6	673·6	26·52	96·22	3·77	Seven
May	6·8	22·7	1·1	29·0	9·8	118·5	52·2	240·1	9·45	34·30	1·35	,,
June	Nil	1·2	Nil	Nil	Nil	Nil	3·0	4·2	0·16	0·60	0·02	,,
July	0·6	1·0	Nil	Nil	Nil	Nil	Nil	1·6	0·06	0·22	Trace	,,
August	Nil	Nil	Nil	Nil	2·8	Nil	Nil	2·8	0·11	0·40	0·01	,,
September	Nil	Trace	Nil	Nil	10·8	Nil	Nil	10·8	0·42	1·54	0·06	,,
October	0·2	2·1	Nil	—	5·6	0·2	24·2	32·3	1·27	5·38	0·21	Six
November	22·7	206·0	4·4	—	7·4	16·2	20·2	276·9	10·9	46·15	1·8	,,
December	120·9	75·0	149·2	—	130·2	207·8	66·0	749·1	29·09	124·83	4·9	,,
Totals	⎰ —	652·9	758·9	—	584·7	1141·7	503·0	mm.				
	⎱ —	25·7	29·87	—	23·02	44·94	19·8	in.				

[1] *Beilage zum Pflanzer,* 1, 3, 4, 12 (1911), 2, 5, 7, 10 (1912); *Vierteljahresbericht der Kaiserlichen Hauptwetterwarte von Deutsch Ost-Afrika,* 2, 3, 4 (1912), 1, 2, 3 (1913); and *Annual Reports: Department of Veterinary Science and Animal Husbandry, Tanganyika Territory,* 1927 and 1928. The — indicates no records.

According to an appendix in *Der Pflanzer,* **8**, No. 6 of 1912, a reprint from *Auskunft über Deutsch Ost-Afrika für Ansiedler und Reisender,* meteorological records had been made at Mpwapwa for nine years, but the above table has been compiled from all the records in the Amani Library, the reprint only giving monthly and yearly averages for the nine-year period.

It will be seen from the above table and chart (Fig. 2) that there is only one rainy season and the heaviest falls (over 4 in.) occur in the months December to April.

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FAUNA.

</div>

The area is not rich in game, there are lions, leopards, a few buffalo, and antelope of various kinds. Birds of various kinds are plentiful.

NATIVE POPULATION.

In the Kikombo Area the native population is not encouraged to settle for animal quarantine reasons, but around Mpwapwa there are numerous scattered settlements of Wagogo and a very few Wanyamwezi.

MPWAPWA T.T.

TEMPERATURES
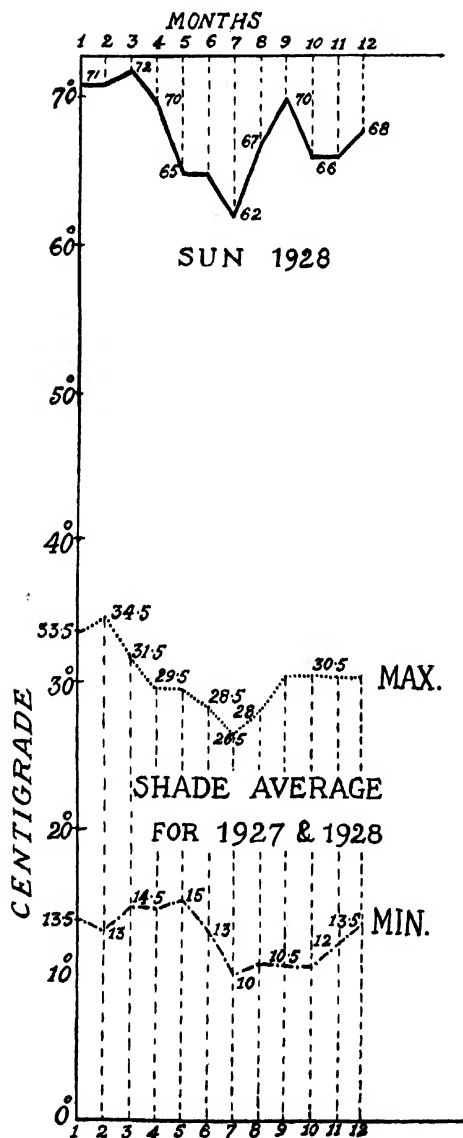
RAINFALL
AVERAGE FOR 6~7 YEARS
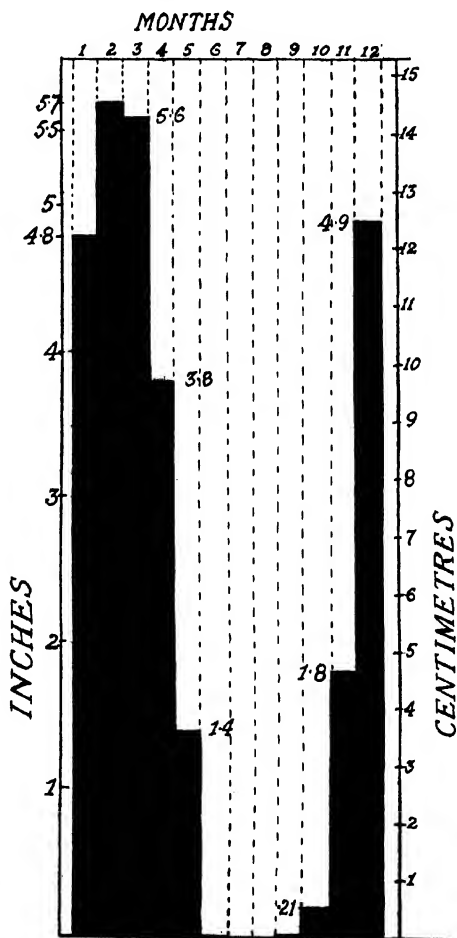
Fig. 2.

The Wagogo are mixed agriculturalists owning herds of cattle, sheep and goats and practising shifting cultivation. On account of the former their settlements are restricted to the proximity of water, although a journey of three or four hours to water in the dry season is not considered too far.

They build long rectangular huts of wattle and daub with flat roofs upon which the produce from their fields is often stored.

Their cattle are penned at night in enclosures made of the stems of *Commiphora* spp. or *Euphorbia Tirucalli* L., which form a living barrier, or they are herded in the court around the three sides of which their hut walls form the barrier, the fourth side being protected by a similar living stockade with a very narrow entrance or exit through which only one animal can pass at a time.

THE VEGETATION OF THE AREA.

The description of the vegetation of Mpwapwa is based on field notes and specimens of which 112 numbers were collected in triplicate, together with others collected by Mr and Mrs H. E. Hornby of the Veterinary Department.

The specimens were preliminarily determined by myself in the Amani Herbarium and the following systematic works were used:

Oliver, D. and others, *Flora of Tropical Africa* (1868–).

Thonner, Fr., *Flowering Plants of Africa* (1915).

Baker, E. G., *Leguminosae of Tropical Africa*, Parts 1–3 (1926–30).

My thanks are due to the Director and the staff of the African section of the Herbarium, Royal Botanic Gardens, Kew, for kindly verifying my determinations and for additional identifications; also to Mr W. Exell of the British Museum (Natural History) for naming the Combretums and to Mr C. E. Hubbard of Kew for specific determinations of the grasses.

The specimens are available for reference at the Herbarium of the East African Agricultural Research Station, Amani, Tanganyika Territory, the Herbarium, Royal Botanic Gardens, Kew, and at the Department of Veterinary Science and Animal Husbandry, Mpwapwa, Tanganyika Territory.

As the area has a dry climate with a somewhat variable but low annual rainfall the vegetation is distinctly xerophytic.

Only two formations are present, the *Deciduous Scrub Formation*[1] with *Cultivated areas* in the formation and a very poor type of *Subtropical Evergreen Forest*. The former is common to the whole area and its plant communities are extremely varied. Of the Subtropical Evergreen Forest a small area occurs on the northern slopes of the Kibariani Mountains.

The observations on these two formations were made during the latter end of August, 1930, from the 16th to 31st, in a rainless month when very little of the vegetation was in leaf. No doubt during the "rains" the whole facies of the vegetation changes, and numerous annual herbs and bulbous and tuberous-

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[1] **Phillips, J.**, "Vegetation Communities in Tanganyika Territory." This JOURN. **18**, No. 2, 201 (1930).

rooted plants of short duration would be in full growth. These were not seen and have therefore not been recorded in this paper.

THE DECIDUOUS SCRUB FORMATION.

On leaving Gulwe Station for Mpwapwa one passes for about ten miles through a very dense community of *Commiphora-Cordyla africana* Lour. with numerous scattered Baobabs, *Adansonia digitata* L.

The Baobabs attain a height of 60 ft. with an immense girth, the others are 30–40 ft. tall, much-branched, bushy trees with hardly any bole development, forming dense stands. Of perennial grasses there appeared to be none, but annual species of *Aristida* and *Eragrostis* were frequent. Other plants in this community were *Balanites tomentosa* Mildbraed and Schlecht., *Delonix elata* Gamble, *Cassia* spp., a succulent spiny *Euphorbia* forming mats on rocks, two other species of succulent *Euphorbia* with sub-simple stems attaining a height of 6 ft. and an occasional candelabra *Euphorbia* with a dense rounded crown, also *Strophanthus Eminii* Aschers. ex Pax (frequent), *Grewia* spp., *Marsdenia* sp. (frequent), *Ziziphus mucronata* Willd., *Z. Jujuba* Lam., and *Combretum* spp. of the sub-scandent shrubby type.

About two miles from Mpwapwa one emerges on to a large open plain under various stages of native cultivation, from areas that had been abandoned for two or three years to areas from which the crops had just been harvested (Fig. 3). This will be described in detail under "Cultivation areas."

In the Kikombo area, the *Adansonia-Strophanthus Eminii* Aschers. ex Pax-*Delonix elata* Gamble community was wanting and replaced by *Acacia-Combretum-Grewia*, *Combretum-Acacia-Commiphora* and *Commiphora-Albizzia-Combretum* communities, all of them very complex and not confined to any particular types of soils.

They usually formed open to closed stands of much branched bushy trees up to 30 ft. tall through which the station stock were pastured. The ground vegetation was very poor; of the grasses, *Cynodon Dactylon* Pers. occurred in favourable situations, while annual *Eragrostis* spp., *Aristida* spp. and *Setaria* spp. were abundant everywhere. The following weeds formed dominant colonies from place to place: *Solanum panduraeforme* Drège ex Dun., *Ocimum americanum* L., *O. suave* Willd., and *Triumfetta* spp.

Of the sub-shrubby plants *Disperma trachyphyllum* Bullock, forming a dense 6 ft. tall scrub, occurred throughout the whole area and in places covered many acres of ground. *Acalypha ornata* Hochst. ex A. Rich. also formed a scrub cover and attained a height of 4–5 ft.; it occurred in the more low-lying areas and was confined to the grey sandy soils. *Croton Menyharti* Pax., *Hoslundia opposita* Vahl and *Lippia asperifolia* A. Rich. were other plants of the scrub but were more local in their distribution.

Of the shrubs and trees the following occurred: *Lonchocarpus capassa* Rolfe, *Afzelia quanzensis* Welw. (very local), *Rhus* spp., *Ziziphus mucronata* Willd.,

Z. Jujuba Lam., *Gymnosporia senegalensis* Loes., *Gymnosporia* sp., *Elaeoden-dron* sp. (evergreen), *Terminalia* sp. (evergreen), *Combretum* spp., *Cordia* spp., *Dombeya* spp., *Lasiosiphon Eminii* Engl. & Gilg., *Vernonia senegalensis* Less., *Capparis Kirkii* Oliv., *C. tomentosa* Lam., *Boscia grandiflora* Gilg., *Courbonia edulis* Gilg. and Benedict (evergreen), *Harrisonia abyssinica* Oliv. (evergreen), *Dichrostachys glomerata* Chiov., and *Thespesia.*

For the community dominants, of the Commiphoras suitable material was not available for collection, but the following were collected: *Combretum*
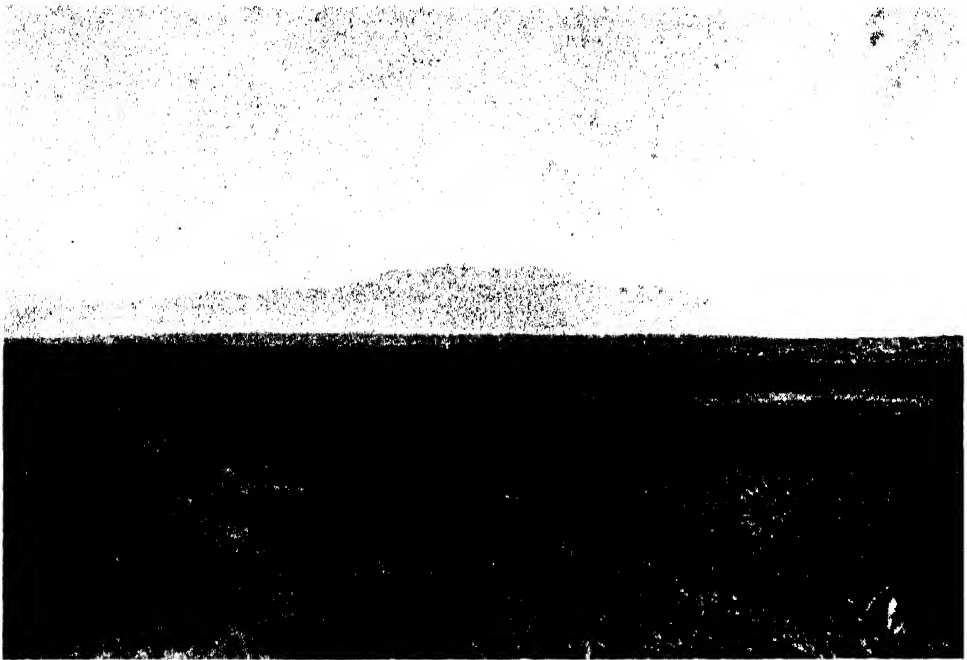
FIG. 3. Open plain under various stages of native cultivation, looking south from Mpwapwa to Gulwe Mountain. The dark line of trees to the left is an avenue of *Cassia siamea* Lam.

Zeyheri Sond. a much-branched bushy tree with large four-winged straw-coloured fruits, *C. Fischeri* Engl. and *C. Brosigianum* Engl. and Diels, bushy shrubs or trees with smaller russet-coloured four-winged fruits, were common.

The Acacias were *A. spirocarpa* Hochst. ex A. Rich., *A. arabica* Willd. and *A. usambarensis* Taub., and the Albizzias *A. Harveyi* Fourn. (*A. hypoleuca* Oliv.), and *A. versicolor* Welw. ex Oliv. locally dominant.

As one ascended the Kibariani Range slopes these communities extended up to about 3800 ft. when one entered the *Berlinia* and *Brachystegia* woodland communities of which there appeared to be three zones.

Berlinia *and* Brachystegia *Woodland* (Pl. III, phot. 1 and Pl. VI, phot. 7).
First zone (3800–4500 *ft. altitude*).

The *Combretum-Acacia-Commiphora* community was gradually replaced by an admixture of *Heeria insignis* Kuntze-*Ormocarpum Kirkii* S. Moore-*Bridelia Niedenzui* Gehrm., bushy, much-branched trees up to about 25 ft. high with a very poor annual grass cover of *Aristida-Eragrostis-Setaria* spp. and a dwarf Cyperacea.

These grasses persisted, but a *Berlinia globiflora* Hutch. and Burtt Davy-*Brachystegia itoliensis* Taub. element, with *Securidaca longepedunculata* Fresen., *Pterocarpus Bussei* Harms., *Dalbergia* sp. near *D. nitidula* Welw. ex Baker, and *Sterculia* spp., became more apparent as one ascended. Of the sub-shrubby herbs *Disperma parviflorum* C. B. Cl. occurred in scattered clumps with *Lippia asperifolia* A. Rich. The following herbs were also noted or collected: *Pogonarthria squarrosa* Pilger, a perennial grass up to 4 ft. tall in scattered clumps, *Kalanchae* spp., *Aloe* sp. near *A. laterita* Engl. (on rocks), *Orobanche ramosa* L. at the base of a *Brachystegia, Viscum Bagshawei* Rendle parasitic on the branches of *Acacia* sp., *Buchnera hispida* Buch.-Ham., *B. longifolia* Klotzsch, *Dicoma sessiliflora* Harv., and a dwarf annual *Polygala.*

Second zone (4400–5500 *ft. altitude*).

In this zone the Brachystegias were dominant; they were more or less flat-crowned trees up to 40 ft. tall with fairly clean boles. The species represented were: *Brachystegia itoliensis* Taub. was the most common; it extends right through the third zone up to 5800 ft. altitude with a consequent reduction in height. *Brachystegia* sp. near *B. taxifolia* Harms., a very beautiful light-crowned tree 30 ft. tall with a smooth brown bark. *B. utilis* Hutch. and Burtt Davy, 30–35 ft. tall with a flat much-branched crown and rough black bark (Pl. III, phot. 1).

Another dominant tree of this community extending from 4000 to 5000 ft. altitude was the much-branched, up to 30 ft. tall, *Combretum Gueinzii* subsp. *splendens* Exell, and in the upper reaches of the zone *Faurea speciosa* Welw. occurred as a much-branched 30 ft. tall tree as well as a very attractive Melastomacea, *Dissotis Melleri* Hook. f. with bright magenta flowers produced at the ends of its branches. This usually grew in rocks and attained a height of 15–20 ft. with stiff erect corky branches. An *Acacia* not unlike *A. Buchananii* Harms., with *Vangueria* sp. was also scattered through the community.

Of the shrubs, the beautiful 6–8 ft. tall *Tecomaria rupium* Bullock occurred on rocks or rocky places from 5000 to 5800 ft. altitude. *Vitex iringensis* Guerke, almost leafless, was also observed. The sub-shrubby herbs, *Heteromorpha arborescens* Cham. and Schlecht. (Umbelliferae), was scattered through the community. *Eriosema ellipticum* Welw. ex Baker, 5 ft. tall, growing in clumps, with yellow flowers, was an abundant plant. Of the herbs, *Helichrysum Kirkii* Oliver and Hiern was common, and *Leonotis mollissima* Guerke,

Phot. 1. *Brachystegia* woodland on upper slopes of the Kibariani Range; compare with Phot. 7.

Phot. 2. Farmland of the Veterinary Department. The two conspicuous clumps of shrubs are *Cassia didymobotrya* Fresen. in a dry river bed.

GREENWAY---VEGETATION OF MPWAPWA

forming fairly large stands, grew in the more open parts of the community with *Euphorbia cyparissioides* Pax, local.

The dominant grasses were, on deep soils, *Hyparrhenia cymbaria* Stapf, 7 ft. tall, forming almost pure stands in open glades, *Themeda triandra* vars. *Burchellii* Stapf, and *hispida* Stapf, 5 ft. tall, with *Cymbopogon excavatus* Stapf. Although these have been included in this zone they extended, in favourable localities, down to 3800 ft. altitude and up to 5500 ft., but have been included here because they were most dominant throughout the zone. In shallow very stony quartz soils a 2 in. tall Cyperacea formed the ground cover together with 3 ft. tall perennial tussock grasses growing in scattered clumps of *Trichopteryx simplex* Hack. and *Diplachne* sp.

Third zone (5400–6100 *ft. altitude*).

Towards the western end of the Kibariani Range, Klippen Mountain, there is a rock escarpment composed of white quartz rocks; on these and below them persisted *Brachystegia itoliensis* Taub. as a 10 ft. tall flat-crowned stunted tree, with *Tecomaria rupium* Bullock as dominants and *Vellozia* sp. (*Barbacenia*), a much-branched shrubby Monocotyledon up to 4 ft. tall, with its stems and branches covered with persistent blackened leaf bases, the apex of the branches being crowned with a tuft of 4–8 grasslike leaves.

The white rocks were covered with a bright red lichen, *Caloplaca murorum* DC., as well as *Usnea cornuta* Koerb. which also formed short pendulous festoons on the *Brachystegia*, giving to the dominant vegetation of the place a weird effect. Other plants of this area were two species of moss, *Camptothecium* and *Leucobryum*; a fern, *Pellaea Goudotii* C. Ch.; *Cineraria kilimandscharica* Engl., *Crassula Illichiana* Engl. and a very dwarf *Oldenlandia Johnstoni* Oliver were herbs growing on the rocks; shrubs, *Asclepias* sp., near *A. Philippsiae* N. E. Br., very local, *Smithia* sp., with orange flowers, 6 ft. tall and dominant in places, and *Myrsine africana* L. was common but scattered. The tussock grass *Trichopteryx simplex* Hack., was also present with the 2 in. high Cyperacea.

Leaving this community and crossing to the eastern end of the range, one passed through *Brachystegia* woodland containing the same grasses as those in the second zone, but an *Acacia* not unlike *Acacia spirocarpa* Hochst. ex A. Rich. with an *Elaeodendron* sp., and *Myrica kilimandscharica* Engl., both trees up to 30 ft. tall with spreading branches and flattish crowns, were present as well as the very hairy *Crotalaria lachnocarpoides* Engl.

To the left of Wald Mountain a native path crosses the range and this passed through a community of *Brachystegia-Uapaca* woodland, the latter an erect, not much-branched 20–25 ft. tall Euphorbiaceous tree with large leathery dark green leaves. In this community there were at least three species of *Protea* which were not in flower, *Agauria salicifolia* Hook. f. ex Oliver, a more or less branched 30 ft. tree of the Ericaceae, and *Osyris abyssinica* Hochst. The

grass cover was very thin and poor in which a tuberous rooted *Aloe* sp., with thin grasslike spiny leaves, grew, and a *Kalanchoe* sp. with pale buff flowers was also present.

In the Deciduous Scrub Formation on the banks of the streams Fringing Bush Communities occurred of which two types can be recognised.

The Kibariani Range forms the main watershed for the area and the streams flow down the southern slopes towards Mpwapwa. Their general direction is south, but those on the eastern side of the Kikombo area curved round and flowed towards the west till they joined the main stream flowing south on the western side of the Kikombo Valley. At the time of my visit four of them had flowing water in their upper reaches, but there were other water channels which were perfectly dry. Those with more or less permanent water did not have such deeply scoured out beds as the dry ones and their banks were not so steep. The dry ones often had cliff-like banks and in places were more than 30 ft. deep.

The two types of Fringing Bush Communities were Evergreen and Deciduous.

Evergreen Fringing Bush Community.

This community is found on the banks of the four streams and deeply scoured water channels, on the former it rarely forms a belt 20 yards wide and on the latter it occupies the cliff-like sides.

The trees attain a height of 60 ft., often with good branch development and thick boles, casting a dense shade under which Rubiaceous shrubs and herbs of the family Acanthaceae abound, with a parasitic Dodder, through which numerous butterflies were flitting. The trees of the community are *Ficus* spp. as dominants, *Acacia campylacantha* Hochst. ex A. Rich. local, *Khaya* sp. frequent and conspicuous on account of its young red foliage standing out above all the other trees, *Parkia* sp., *Garcinia* sp., *Euclea* sp., *Chrysophyllum* sp., *Maesa lanceolata* Forsk., *Syzygium cordatum* Hochst., *Lonchocarpus capassa* Rolfe, *Baphia* sp. and *Sorindeia obtusifoliolata* Engl.

Two rare trees in the community were *Pleomele Papahu* N. E. Br. (Liliaceae) and *Pygeum africanum* Hook. f. (Rosaceae). The former is a common tree in the Evergreen Rain Forest of the Usambaras and the latter according to Battiscombe[1] is widely distributed in the forests of the highlands of Kenya from an altitude of 6500–8000 ft., attaining its maximum development in forests subject to heavy rainfall. The presence of these two species together with *Maesa lanceolata* Forsk. is significant; they may be relics of Rain Forest which covered the whole area in past times when the rainfall may have been much heavier than it is to-day.

Lianes: *Combretum padoides* Engl. and Diels, *Landolphia* sp., *Hippocratea obtusifolia* var. *Richardiana* Loes., *Secamone* sp. and *Clematis simensis* Fresen.

Scandent shrubs: *Cardiogyne africana* Bur., *Capparis tomentosa* Lam., and *Renschia mirabilis* Bullock (very local), and *Vernonia aurantiaca* N. E. Br.

[1] *Descriptive Catalogue of Common Trees and Woody Plants of Kenya Colony*, p. 46 (1926).

Phot. 3. Native cultivation: first year after clearing, crops just harvested.

Phot. 4. Native cultivation: after several years cultivation; crop has been harvested and cattle browsed through. Trees are *Acacia spirocarpa* Hochst. ex A. Rich.

GREENWAY—VEGETATION OF MPWAPWA

Herbs: the Acanthaceae are the most representative of the community and the following also occur: *Impatiens Hochstetteri* Warb., *Mellera submutica* C. B. Cl., *Moschosma polystachyum* Benth.; *Adiantum* sp., *Ranunculus pubescens* Thunb., *Equisetum ramosissimum* Desf. together with *Cyperus flabelliformis* Rottb., and *Pennisetum purpureum* Schum. occurring as water side plants.

Deciduous Fringing Bush Community.

This community succeeds the Evergreen Fringing Bush below the limits of the permanent flowing streams which during the dry season retreat towards the hills.

Often *Capparis tomentosa* Lam. occurs with other evergreens such as *Vangueria* sp., *Cordia* sp., and *Ficus* spp.; the dominant trees are *Acacia albida* Del., *A. campylacantha* Hochst. ex A. Rich., and *Albizzia Harveyi* Fourn., with *Tamarindus indica* L., *Kigelia aethiopica* Decne., *Ferdinandia magnifica* Seem. less frequent. The shade cast by these is extremely light. The community often contains scandent shrubs of *Phyllanthus reticulatus* Poir., *Plumbago zeylanica* L., an orange-flowered Composite, *Vernonia aurantiaca* N. E. Br., *Clematis simensis* Fresen., *Blepharis* sp. and *Dalbergia* sp. Other plants of this community are *Cassia didymobotrya* Fresen., *Ipomaea* sp., *Indigofera* spp. and *Boerhaavia* spp., and the grasses *Cynodon Dactylon* Pers., *Panicum maximum* Jacq., *Pennisetum purpureum* Schum. and *Phragmites communis* Trin. are also present but in very scattered stands.

In this Deciduous Fringing Bush Community mention must be made of a stand of *Acacia campylacantha* Hochst. ex A. Rich.-*Disperma trachyphyllum* Bullock-*Acalypha ornata* Hochst. ex A. Rich. which occurs on the south eastern side of the Kikombo Valley. It appears to occupy an area of what was the flood plain of the Nkunda and Kibariani streams or the basin of a very shallow lake. Its soil type is a grey, almost white sandy soil with small rounded pebbles. The *Acacia campylacantha* Hochst. ex A. Rich. attains a height of 40 ft., but appears to be dying out; the *Disperma trachyphyllum* Bullock and *Acalypha ornata* Hochst. ex A. Rich. form a dense cover 6 ft. tall which it is impossible to penetrate. Other trees found here are *Deinbollia nyikensis* Baker, *Acacia spirocarpa* Hochst. ex A. Rich., *Ficus* sp. near *F. Stuhlmannii* Warb. and *Kigelia aethiopica* Decne., these latter three on the banks of a dried up stream which cuts through the area.

CULTIVATED AREAS.

The cultivated areas are of two kinds, European and native.

European.

The Veterinary Station proper was composed of farmland with paddocks and the gardens of the staff.

The farmland is reserved for the cultivation of maize, teff, Sudan grass and beans as supplementary feeding material for the stock during the dry season (Pl. III, phot. 2).

The paddocks are sown down with teff and allowed to revert back to grass. The grass is *Cynodon Dactylon* Pers. which, in August, formed a very poor and thin ground cover. It requires constant attention to prevent over-grazing and the invasion of thorny shrubs such as *Acacia* spp. and *Dichrostachys glomerata* Chiov., and weeds like *Ocimum* spp. and *Solanum panduraeforme* Drège ex Dun., taking its place.

With constant care, much watering, and ceaseless warfare against white ants, an attractive garden can be made and the following plants were noted:

Fruits.

Mango, guava, coconut, papaw, orange, lemon, Avocado pear and banana.

Vegetables.

Beetroot, carrots, cabbage, beans, peas, lettuce, tomato, etc.

Flowering plants.

Trees. Casuarina equisetifolia L., *Delonix regia* Rapin., *Cassia siamea* Lam., *Albizzia Lebbek* Benth., *Adenanthera pavonina* L., and *Jacaranda* forming a pole-like growth without branching.

Shrubs. The hedge plants were *Caesalpinia pulcherrima* Sw., *Dodonaea viscosa* Jacq. and *Euphorbia Tirucalli* L.; while such shrubs as *Acalypha*, *Bauhinia* spp., *Melia Azedarach* L., *Euphorbia pulcherrima* Willd. ex Klotz., *Tecomaria capensis* Spach., *Lantana* sp., *Tecoma* sp., *Plumeria* sp. and *Nerium Oleander* L., made an attractive display.

Herbs.

Cannas, carnations, antirrhinums, dahlias, zinnias, sweet peas, aloes, petunias, etc., could also be grown.

The lawns were composed of *Cynodon Dactylon* Pers., and like most lawns had a weed which in this case was a very low-growing herb, *Euphorbia hirta* L.

Native.

The Wagogo, like most African tribes, practise shifting cultivation. In opening up fresh areas for cultivating they select a site in the Deciduous Scrub Formation and proceed to stump every tree to within 3–12 ft. from the ground (Pl. V, phot. 5), and cut down all bushes. The Baobab is always left, no doubt, on account of its great size and economic importance to the natives. Other trees are sometimes left, possibly on account of the hardness of their woods, or for shade purposes, usually *Acacia spirocarpa* Hochst. ex A. Rich. and *Ostryoderris Stuhlmannii* Dunn ex Baker f.

When cutting and felling has been completed the cuttings may be piled into heaps and fired, or they may be fired *in situ* and the site is then ready for planting. In this area the chief crops in order of importance are ground nuts, maize, millets (*Pennisetum spicatum* Roem. and Schult. and *Sorghum caudatum* Stapf), beans with a little pigeon pea, tobacco and gourds.

Phot. 5. Native cultivation in Deciduous Bush Formation: first year of clearing.

Phot. 6. The eastern end of the Kibariani Range, looking towards the
highest point, 6100 ft. altitude.

GREENWAY—VEGETATION OF MPWAPWA

The site is cultivated for a period of 3–6 years, sometimes less, sometimes more, a great deal depending upon the fertility of the soil, after which it is abandoned and another site selected (Pl. IV, phots. 3 and 4).

An abandoned site is immediately invaded by annual weeds such as *Tragus racemosus* All., *Eleusine indica* Gaertn., *Aristida adscensionis* L., *Eragrostis aspera* Nees (abundant), *Dactyloctenium aegyptium* Beauv., *Leptocarydion Vulpiastrum* Stapf (abundant) and *Rhynchelytrum roseum* Stapf and Hubbard amongst the grasses; *Cleome hirta* Oliver, *Gynandropsis gynandra* Briq. (abundants), *Sesbania* sp., an 8 ft. tall annual with yellow-brown spotted flowers, very abundant, *Blumea aurita* DC. (abundant), *Ageratum conyzoides* L., *Astrochlaena hyoscyamoides* Hallier f. ex Engl. (very abundant) and *Sesamum angustifolium* Engl.

This community is gradually invaded by *Acacia* spp., *A. spirocarpa* Hochst. ex A. Rich., *Dichrostachys glomerata* Chiov., *Ostryoderris Stuhlmannii* Dunn ex Baker f., *Lonchocarpus capassa* Rolfe, scandent *Combretum* spp., *Vitex iringensis* Guerke and shrubby Capparids, amongst which, various species of *Ipomaea* such as *I. involucrata* Beauv., *I. mombassana* Vatke, *I. Pes-tigridis* L., *I. obscura* Ker and *I. Whyteana* Rendle form a dense tangle.

After a long period these abandoned cultivated areas, no doubt, revert to the Deciduous Scrub Formation, but apparently the area at Mpwapwa is not allowed to do this and is put under cultivation before it reaches its climax type of vegetation.

THE SUBTROPICAL EVERGREEN FOREST FORMATION.

On the northern slopes of Wald Mountain at an altitude of 6100 ft. a patch of forest occurred (Pl. V, phot. 6). As only the fringe of it was entered it is not proposed to describe it in much detail.

The fringe was composed of a practically pure stand of a 30 ft. tall, much-branched Celastraceous trees of *Gymnosporia* sp. or *Elaeodendron* sp. with thorny branchlets. Their crowns were flat and interlaced, casting a fairly dense shade with very little undergrowth. The branches were covered with moss and the ferns *Polypodium lanceolatum* L., *Asplenium theciferum* Mett. were epiphytic upon them; another fern, *Dryopteris mollis* Hieron., grew upon the ground. Above this dense canopy the scattered crowns of an *Albizzia* sp. projected, and further down the slopes to the north in the valleys other species of taller trees occurred. Fringing this forest on its upper limits and the adjoining *Brachystegia-Uapaca* woodland was a tangled belt of vegetation composed of bracken, *Pteridium aquilinum* Kuhn, the grasses *Panicum maximum* Jacq. and *Setaria Chevalieri* Stapf, with a *Rubus* sp. and showy herbs such as *Hypoëstes antennifera* S. Moore, *Achyrocline Schimperi* Sch. Bip. ex A. Rich., *Erlangea* sp. near *E. ruwenzoriensis* S. Moore, *Pavonia Schimperiana* Hochst. ex A. Rich. and *Abutilon longicuspe* Hochst. ex A. Rich., with scattered trees of *Cussonia* sp.

The above is a description of the vegetation in a very small area of the Central Province, Tanganyika Territory, in which the natives practise a mixed agriculture and in which the problem of over stocking and shortage of grazing is becoming very acute.

According to a livestock census the people of the Province owned in 1928[1]: cattle 1,177,842; sheep and goats 1,185,810; pigs 169; donkeys 10,189; horses 5; mules 3, of which the stock at Mpwapwa form a very small fraction.

The question naturally arises, "What do these animals find to live on during the dry season?" There are no grasslands at Mpwapwa and of the following grasses that have been collected the majority are very poor for grazing or fodder purposes:

Aristida adscensionis L.
A. Steudeleana Trim. and Rupr.
Brachiaria brizantha Stapf
B. regularis Stapf
B. serrifolia Stapf
Cymbopogon excavatus Stapf
Cynodon Dactylon Pers.
C. plectostachyus Pilger
Dactyloctenium aegyptium Beauv.
Diplachne sp.
Eleusine indica Gaertn.
Enteropogon macrostachyum Munro
Eragrostis aspera Nees
Heteropogon contortus P. Beauv. ex Roem. and Schult.
Hyparrhenia cymbaria Stapf
H. filipendula Stapf

Leptocarydion Vulpiastrum Stapf
Panicum brevifolium L.
P. deustum Thunb.
P. maximum Jacq.
Pennisetum ciliare Link.
Pogonarthria squarrosa Pilger
Rhynchelytrum roseum Stapf and Hubbard
Setaria homonyma Chiov.
S. pallidifusca Stapf and Hubbard
S. verticillata P. Beauv.
Sporobolus festivus Hochst.
S. indicus R. Br.
Themeda triandra Forsk. var. Burchellii Stapf
T. triandra var. hispida Stapf
Tragus racemosus All.
Trichopteryx simplex Hack.
Urochloa trichopus Stapf

Of the above 33 species *Brachiaria brizantha* Stapf, *Cynodon Dactylon* Pers., *Dactyloctenium aegyptium* Beauv., *Heteropogon contortus* P. Beauv. ex Roem. and Schult. (when young), *Hyparrhenia cymbaria* Stapf (when young), *Panicum maximum* Jacq., *Setaria pallidifusca* Stapf and Hubbard and *Themeda triandra* Forsk. are recorded as good forage grasses, but their distribution throughout the area is extremely local.

Cynodon Dactylon Pers. occurred in the low-lying parts of the area; *Hyparrhenia cymbaria* Stapf forms pure stands together with *Themeda triandra* Forsk. in the *Brachystegia* woodland on the slopes of the Kibariani Range above the limits, about 3800 ft. altitude, of the grazing radius of the stock and therefore is of no value on account of its inaccessibility.

It has been observed that where stock are able to penetrate to this area these two species are soon eaten out and annual *Aristida* and *Eragrostis* spp. take their place; the next phase in the succession is a dense growth of thorny shrubs such as *Acacia* spp., *Dichrostachys glomerata* Chiov. and *Commiphora* spp., because the limiting factor to the development of these species, fierce grass fires, has been removed. In association with these thorny shrubs the regenerating *Berlinia-Brachystegia* spp. form a fairly dense stand of coppice growths

[1] *Annual Report: Department of Veterinary Science and Animal Husbandry, Tanganyika Territory*, p. 35 (1928).

Phot. 7. *Berlinia Brachystegia* woodland on upper limits of cattle-grazing range. Note coppice-like growths, and compare with Phot. 1.

GREENWAY—VEGETATION OF MPWAPWA

up to 20 ft. tall with thin stems (Pl. VI, phot. 7). This, no doubt, would form in this area *Brachystegia* woodland again with *Hyparrhenia cymbaria* Stapf and *Themeda triandra* Forsk. stands, if stock were prevented from grazing through them.

Towards the end of the dry season after the crops have been harvested, about the end of July and August, the areas of native cultivation are available as browsing grounds for the native cattle. The dried stems and leaves of the ground nuts, maize, millets, beans, and fruits of gourds, provide valuable feeding material, but no effort is made to conserve them, and the animals browse through this fodder over and over again until all has been eaten.

It is obvious from these observations that the cattle cannot be entirely dependent on the grasses for forage, and these are supplemented by the fruits and leaves of certain trees, shrubs and herbs in the area.

A PRELIMINARY ACCOUNT OF THE AQUATIC AND SUB-AQUATIC VEGETATION AND FLORA OF THE WITWATERSRAND

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(With Plates VII and VIII, one Folding Figure and two Figures in the Text.)

CONTENTS.

INTRODUCTORY.

THERE are many natural, semi-natural and artificial sheets of water on the Witwatersrand, and the object of this research is to give an account of the aquatic and sub-aquatic communities which occur in and around these sheets of water.

The investigation was suggested to me by the late Prof. C. E. Moss, of the University of the Witwatersrand, Johannesburg, all the work being done under his guidance. Determinations of the vascular plants were made by him. The Characeae were determined by Mr J. Groves, and the phytoplankton by the late Dr C. H. Ostenfeld of Copenhagen. Numbered specimens of the vascular plants, and of the Characeae are preserved in the herbarium of the University of the Witwatersrand, and specimens of the plankton collections are in the botanical museum of the same university.

I. PHYSIOGRAPHY.

The sheets of water investigated are on the Witwatersrand, extending from Florida Lake on the west of the Central Rand, to the Brakpan pans on the far Eastern Rand. Florida is nine miles to the west of Johannesburg and Brakpan twenty-three miles to the east (Figs. 1 and 2).

Phot. 1. Brakpan. Main pan. 28 July 1929. A permanent pool at the south of the pan. The samples of plankton mentioned in the text were collected here.

Phot. 2. A permanent pool in the Brakpan main pan. The pools are constructed.

Phot. 3. A permanent pool and ditches in the pan at Brakpan. The light-coloured floating vegetation near the steep bank in the right centre is *Potamogeton pectinatus*. February 1927.

The country in which these sheets of water occur, forms part of the "high-veld" of South Africa, and lies at an elevation of between 5000 and 6000 ft. The range of elevation within the area is about 1000 ft., and the surface is varied and diversified by numerous hills and escarpments. The Witwatersrand forms one of the main watersheds of South Africa (Mellor, 1917). There are no rivers of any considerable size, but the area is watered by numerous small streams which originate in this elevated ridge. From the northern slopes these streams flow into the Crocodile or Limpopo River, and finally into the Indian Ocean. These northward flowing streams have steeper gradients than those flowing southwards, and have cut narrow gorges or kloofs through the ridge. The Witpoortje gorge, north-east of Krugersdorp, is an example of this. Here the stream passes through a deep and narrow gorge into the lower country, consisting of a rather flat plateau of ancient granite. The southern slopes give rise to streams which flow into the Klip River, which joins the Vaal River, whose waters reach the Atlantic Ocean. These southward flowing watercourses follow more open valleys and their descent into the lower country is more gradual. The streams which form Canada and Florida lakes meet near Nance-field and then flow into the Klip River.

The natural sheets of water are streams and pans. All the lakes investigated, namely, Florida, Boksburg, Geduld and Wemmer lakes (the last being usually known as Wemmer pan), are semi-natural, since they have been formed by the construction of a wall on one side of each stream, and are in reality merely wider portions of the streams themselves.

The dams are artificial, being entirely of human construction and are used by the mines and other industrial concerns.

The lakes and dams are permanent. The pans are temporary and dependent on the rainfall for their supply of water. In the Eastern Transvaal, however, there are some pans in the Bethal and Ermelo districts which are permanent, owing to the fact that they have streams, and in some cases springs, feeding them.

Pans.

On the Far Eastern Rand, the surface beds of which consist of coal-measure rocks belonging to the Karroo system, numerous pans occur. The pans are shallow, and more or less circular depressions with almost level floors. They range in length and breadth from a few yards to a few miles.

Various views as to the origin and mode of formation of pans have been put forward. M. S. Alison (1899) suggests that pans were formed by zoogenous erosion. Passarge (1904) also shows the important part played by herds of wild animals in forming and deepening pans by the removal of mud and substances in solution from the drinking places. It is possible that the animals caused deepening of the pans, but the beginnings of the pans probably were already there when the animals visited the drinking places. A. W. Rogers
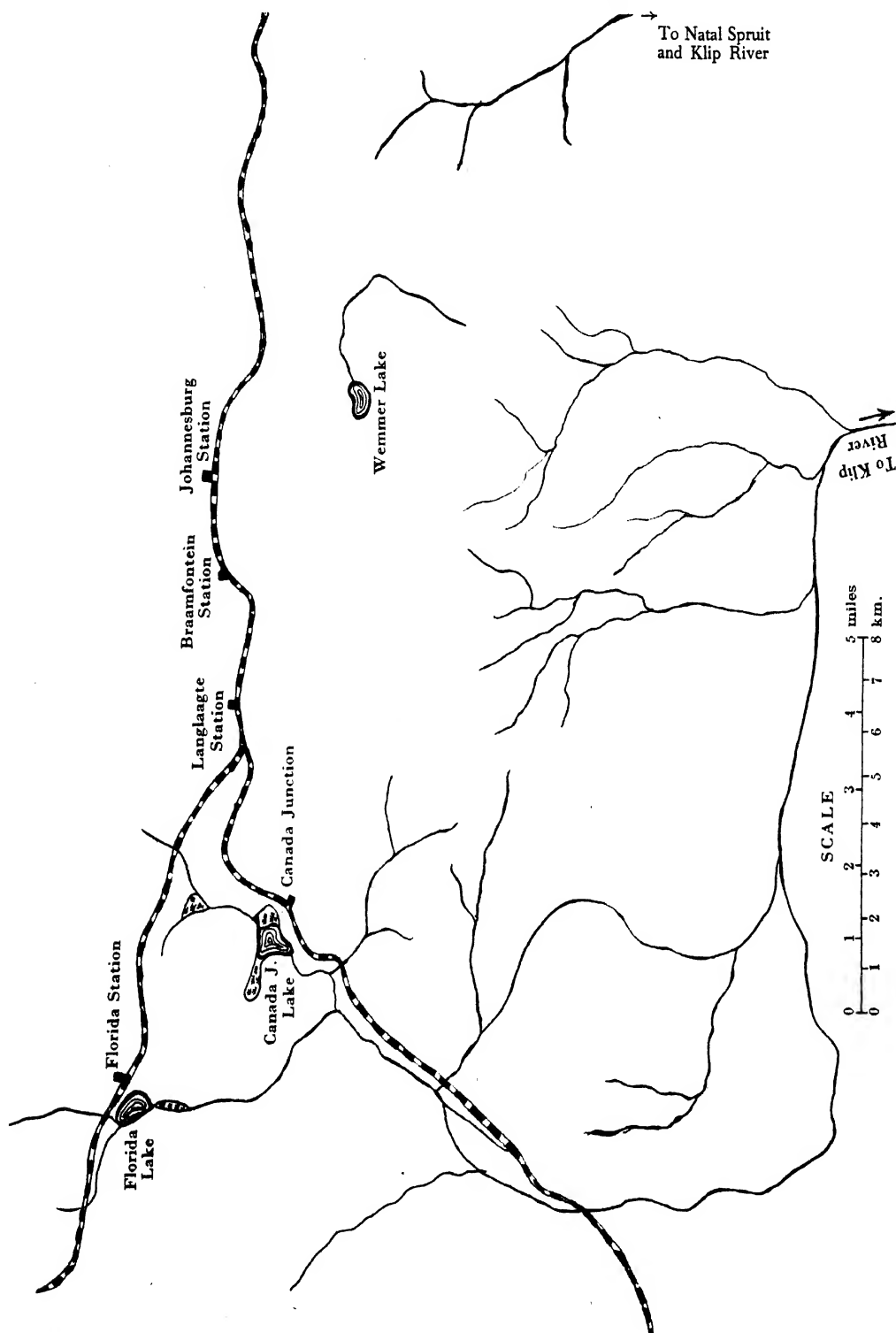
Fig. 1. Sketch map of Central Rand showing locations of lakes. Based on the Union of South Africa Department of Mines and Industries Geological Survey Sheet 52, Johannesburg.
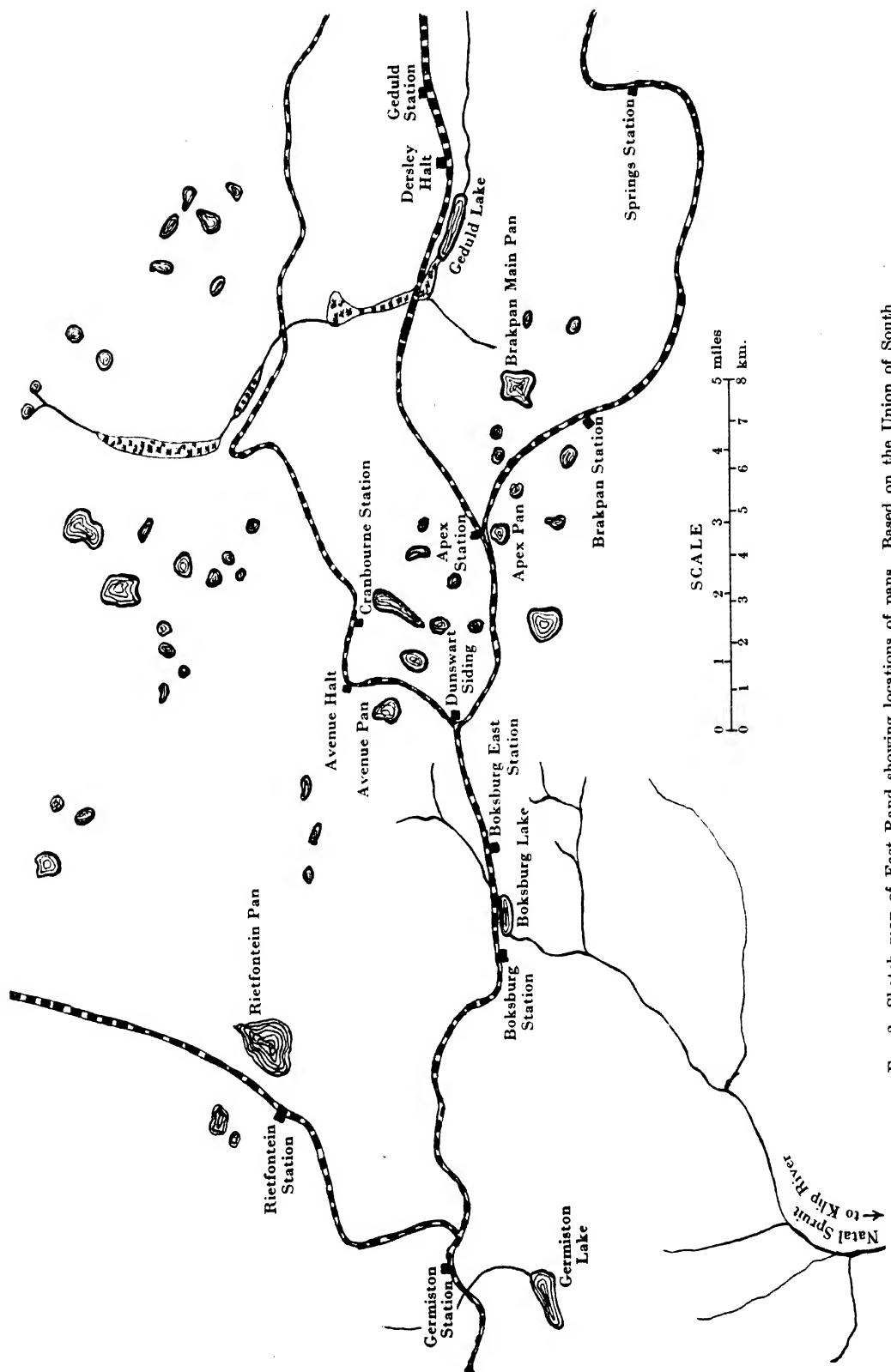
Fig. 2. Sketch map of East Rand showing locations of pans. Based on the Union of South Africa Department of Mines and Industries, Geological Survey Sheet 52, Johannesburg.

(1922) considers that pans were formed by wind erosion at a time when the climate of the country was drier than it is now. He considers that pans can be formed by wind erosion alone, and that wind erosion is aided by the hindering and prevention of vegetation over the pan floor, due to brackishness of the soil. Rogers (*loc. cit.*) quotes Penck (1909), who argued that the pans in the Transvaal and Orange Free State were formed when these parts of the country had a drier climate than they have at present, because the pans could not have been developed in a humid climate. E. H. L. Schwartz (1925) considers that pans are formed in the following way: To a large extent South African rivers are intermittent, that is, they flow for a short period during the year, namely during the rainy season. The smaller rivers are frequently dry. The water which falls is not sufficient to fill the river channel, but there is an excess where the storm breaks, causing the river to overflow its banks and to form a temporary "vlei" or marsh. Storms break more or less in the same place, and thus eventually the marsh is widened. If there is not sufficient water to flow past this marsh for some time, depressions are formed in this widened part of the river channel, by weathering and disintegration of the underlying rocks. When the water dries, a powdery soil is left, which is blown about by the wind, and this causes deepening of the pan.

Over very flat country (and the pans considered in this paper are all in comparatively flat country) the depressions forming the stream courses may be very slight. As a matter of fact, the watercourses in the coal-measure country have no definite channels, and take the form of swampy marshes which are dry in winter. Perhaps from such swampy marshes the East Rand pans have originated. There is, however, no connection between the pans to indicate that they are parts of a river channel, and they therefore give no definite indication as to their origin. On the other hand, pans in the Ermelo district, of which "Lake" Chrissie is the largest, seem to be connected and are, perhaps, parts of a river system. In May, 1928, at the close of the rainy season, I noticed that three pans, one of which had a spring entering it, were almost connected. These pans were not far apart and the spaces between them were swampy. The first pan had a spring entering it and is probably the beginning of a river which, owing to insufficient water, flowed no further than the third pan. Although the climate is humid (the average rainfall is about 31·28 in.; Lewis, 1925) there does not appear to be enough water to fill the watercourse. Rogers (*loc. cit.*) finds it difficult to account for the origin of these pans in the Ermelo district by wind erosion, because the climate is humid and the soil not sufficiently brackish to prevent the growth of vegetation. The pans in this district which become dry in winter are covered with *Phragmites communis* Linn.

In the case of Verneuk pan at Kenhardt, which is a great flat tract, 17 miles long and 6 miles wide, Rogers (1911) considers the extremely low grade reached by streams behind bars of hard rock, the unfavourable conditions for plant growth due to brackishness of the soil, and finally the scope given to wind to

remove dust and sand from the bare ground, as being responsible for the formation of the pan. Of the temporary pans there are two kinds; pans with mud floors, an example of which is the Avenue pan, and pans with grass floors, like the Rietfontein and Brakpan pans. Pans with grass floors support a rich growth of vegetation even when they are dry. In the main pan at Brakpan the floor is covered with *Cynodon transvaalensis* Burtt Davy, which forms an attractive and natural lawn. Other grasses occurring in these grass pans are: *Diplachne* sp.nov., *Panicum coloratum* Linn., *Panicum laevifolium* Hack and *Tragus* sp. This covering of vegetation in the pan when it is dry hinders wind erosion.

The mud pans such as the one at Avenue, have, when dry, bare floors of dark mud, which is easily wind borne. It is interesting to note that the mud pans are deeper than the grass pans. Wind erosion, when not hindered by a covering of vegetation over the pan floor seems to cause deepening of the pan.

A white incrustation of salts is commonly found on the receding margins of the pans, as the waters are drying up, and on the floors of the pans when they are dry. Rough analyses of these salts indicate that the incrustations contain very large amounts of sodium chloride, small amounts of calcium carbonate and traces of magnesium sulphate.

II. Aquatic Plant Communities.

The aquatic plant formation includes the plant life of all the aquatic habitats such as lakes, streams, pans, and dams. The vegetation differs considerably in the different types of sheets of water. What the actual determining factors are it is difficult to state, but it is probable that the leading factors are aeration of the water and the amount of dissolved mineral and organic substances in the water (Moss, 1911).

C. E. Moss (1913) pointed out that the chemical constituents of the soil, in addition to any or all of the physical conditions, have, directly and indirectly, great influence on the differential distribution of the flora and vegetation of a district. It is probable that the chemical and physical conditions of the waters are determining factors, but the present state of knowledge regarding the waters of the Witwatersrand, and the data ascertained, do not allow of any detailed statement.

Taking aeration and amount of dissolved mineral salts as leading factors, and following C. E. Moss (1911), the aquatic communities can be divided into the following:

(1) Communities of still waters, such as the pans. These have a high mineral content, the concentration increasing as the dry season approaches.

(2) Communities of slowly flowing waters such as the semi-natural lakes.

(3) Communities of rapidly moving waters, namely the streams, which are relatively poor in mineral salts and rich in oxygen.

The aquatic communities of the sheets of water investigated include the following:

A. Free-floating communities:

  (a) Plankton.

  (b) Spermatophyta.

B. Communities of rooted plants entirely submerged.

C. Communities of rooted and submerged plants with floating leaves.

D. Reed swamp communities.

The sub-aquatic communities include:

A. Hemi-halophytic communities.

B. Marsh communities.

The former are of very limited extent, the latter are common and extensive.

A. *Free-Floating Communities.*

(a) *Plankton.* This consists of minute plants which float in the water. The organisms are unicellular, multicellular, solitary or colonial. Some of the algal free-floating organisms differ from true plankton by floating on the surface of the water, by being adapted to existence in contact with air, and forming, in some cases, scums. Warming (1909) places these plants together with the free-floating Spermatophyta in a separate formation, the hydrocharid formation or pleuston. In the hydrocharid formation occur various Chlorophyceae, such as *Spirogyra* sp., *Zygnema* sp., and *Hydrodictyon* sp. (probably the recently described *H. indicum*). False plankton is formed by Chlorophyceae, which are at first epiphytic, usually on members of other communities, but which later become free, when they float on the surface of the water buoyed up by the oxygen which they evolve. This group is represented by species of *Spirogyra*, *Mougeotia*, *Zygnema*, *Oedogonium*, and *Draparnaldia* (from Brakpan pan). These plants occur in both fresh and stagnant waters. They are especially abundant in sheltered areas, such as in the open reed swamps. *Batrachospermum* sp. occurs in streams at Florida and Witpoortje.

In a permanent pool in the main pan at Brakpan, the following occurred. The frequency symbols used are: c. common, v.c. very common, r. rare, v.r. very rare.

Samples collected on September 7th, 1927.

Closterium sp.	c.	Lyngbya limnetica Lemm.	v.r.
Cosmarium sp.	r.	Oscillatoria sancta Kg.	v.r.
Cyclotella Meneghiniana Kg.	r.	Scenedesmus armatus Chod.	v.r.
Gomphosphaeria aponina Kg.	r.	Tetraedron minimum Hansg.	v.r.
Merismopedia spp.	v.r.		

Samples collected on February 19th, 1929.

Ankistrodesmus falcatus Ralfs, var. spirilliformis G. S. West	v.r.	Eudorina n.sp.	v.r.
Characium limnetica Lemm.	v.r.	Pediastrum pertusum Kg.	v.r.
Eudorina elegans Ehrb.	v.r.	Microcystis aeruginosa Kg.	v.r.

Samples collected on March 11th, 1928.

Eudorina sp.	r.	Pediastrum pertusum Kg.	v.r.
Eudorina elegans Ehrb.	r.	Volvox Rousseleti G. S. West	v.c.

Samples collected on April 15th, 1928.

Eudorina elegans Ehrb.	c.	Pediastrum pertusum Kg.	v.r.
Coelastrum pulchrum Schm. var.		Pediastrum sp.	r.
intermedium Bohlin	v.r.	Plectonema sp. (perhaps n.sp.)	r.
Cyclotella Meneghiniana Kg.	v.r.	Volvox Rousseleti G. S. West	c.

Samples collected on May 6th, 1928.

Eudorina elegans Ehrb.	c.	Volvox Rousseleti G. S. West	v.c.

Limnoplankton is found in fresh waters such as Florida Lake and Geduld Lake. In samples of plankton collected at these lakes the following occurred:

Samples collected at Florida Lake on August 28th, 1927.

Coelastrum pulchrum Schm. var.		Mallomonas acaroides Perty	v.r.
intermedium Bohlin	r.	Peridinium tabulatum	v.r.
C. reticulatum Lemm.	v.r.	Phacus pleuronectes Duj.	v.r.
Dinobryon divergens Imhof var.	v.c.	Tabellaria flocculosa Kg.	v.r.
Melosira ambigua O. Muller	v.c.		

Samples collected at Geduld Lake on March 30th, 1928.

Ankistrodesmus falcatus Ralfs, var.		Scenedesmus quadricauda Breb.	v.c.
spirilliformis G. S. West	v.r.	S. opoliensis Richter	v.r.
Pediastrum boryanum Meneg.	r.	S. dimorphus Kg.	v.r.

Saproplankton occurs in stagnant pools and also in swamps. The swamp at the north of the main pan at Brakpan often has a covering of about 4 in. of water. Here occur three species of *Euglena*, *Oscillatoria sancta* Kg. which sometimes forms thick mats on the ground, and *Microcystis pulverea* Mig. The last mentioned occurs as a pink gelatinous free-floating mass. *Microcystis aeruginosa* Kg. also occurs in stagnant pools forming a bright green scum on the surface of the water. It has been found in a stagnant pond in the Johannesburg Zoological Gardens.

The determinations of the Algae are not complete. The late Dr Ostenfeld passed on the samples, together with Algae collections from other localities in the Transvaal, to Mr Nygaand, who published an account of these collections in a series on the Fresh-water Algae of South Africa (Nygaand, 1932).

(b) *Spermatophyta*. Free-floating Spermatophyta include *Utricularia stellaria* Linn., which occurs in the pans at Brakpan and Rietfontein, *Lemna gibba* Linn., *Lemna minor* Linn., and *Wolffia arrhiza* Wimmer. *L. gibba* and *L. minor* occur in the Avenue pan and also in a permanent ditch in the main pan at Brakpan. *Wolffia arrhiza* is found in a swamp between State Mines and Modder B. The Lemnaceae were found flowering in May and June, 1928.

B. *Communities of Rooted Plants entirely Submerged.*

Chara braunii Gmelin occurs in the pans at Brakpan and Rietfontein.

Chara fragilis Desvaux is found in the Brakpan pans.

Chara stachymorpha Ganterer occurs in Florida and Boksburg lakes.

Nitella doidgeae Groves and Stephens is found in Florida and Boksburg lakes.

Nitella dregeana Kutz. occurs in the Brakpan pans.

Nitella hyalina Ag. also occurs in the Brakpan pans.

Lagarosiphon muscoides Harvey occurs in the pans at Brakpan and Rietfontein, in Boksburg Lake and in Florida Lake.

Lagarosiphon major Moss occurs at Springs, at Birchleigh and at Florida Lake.

L. muscoides and *L. major* were fully described by V. A. Wäger (1928). In the case of *L. muscoides*, Wager considers that there are two different habitat forms of the same species due to different external conditions. These two forms he calls *L. muscoides* forma *brevifolia*, which perhaps results from growth in unfavourable conditions of light and temperature, and *L. muscoides* forma *longifolia*, growing in optimum conditions of light and temperature.

Potamogeton pectinatus Linn. is found in the pans at Brakpan and Rietfontein and in the pan at Apex. It also occurs in Geduld Lake. Specimens from Brakpan have been identified as *Potamogeton pectinatus* Linn. var. *diffusus* forma *laxus* Hagstrom, by the late Mr Arthur Bennett. The plant overwinters by the formation of tubers on special branches, and where the water does not dry up in winter the plant is evergreen.

Potamogeton nodosus Poir. occurs on the north-west side of Florida Lake.

Potamogeton badius Hagstrom occurs in Florida Lake and in a pond at Birchleigh.

Potamogeton sp.nov. also occurs in Florida Lake. I have not found this plant. It was found in March, 1923, by Prof. Moss who describes the fruit as follows: "The fruit is abundantly warted on the central carina, with two bosses on the ventral side. The sides are flat, not impressed. The fruit is 0·3 cm. long and 0·25 cm. broad."

Zannichellia pedicellata Fries occurs in the main pan at Brakpan, where it is dominant in communities in the permanent ditches at the north side of the pan.

Scirpus fluitans Linn. is widespread, occurring in all the sheets of water investigated. The plant has transitional forms, existing as a marsh plant, and when it is submerged, as an aquatic with submerged leaves. The leaves in the submerged form become long and strap-shaped, reaching a length of 30–40 cm.

C. *Communities of Rooted and Submerged Plants with Floating Leaves.*

Ilysanthes conferta Hiern is found in a small pan at Rietfontein: the floating leaves form a rosette of eight to ten.

Limnanthemum thunbergianum Grisebach is found in Florida Lake, forming dominant associations in the sheltered regions of the lake, as in the open reed swamp, and also as a zone at the edge of the closed reed swamp. It also occurs in the backwater of the stream at Canada about one mile from Canada Lake. Portions of the plant broken off and reaching the margin of the lake exist as mud forms. The petiole then becomes much shorter, and the lower surface of the leaf touches the ground.

Marsilia macrocarpa Presl occurs in the permanent pools in the pans at Brakpan and Rietfontein, in Boksburg and Geduld lakes. In permanent waters the plant occurs all the year as an aquatic. In temporary sheets of water it exists as a marsh plant when the water dries (Roux, 1929).

Polygonum amphibium Linn. is found in the large pan at Rietfontein and at Geduld Lake. The plant grows as a sub-terrestrial and can readily adapt itself to an aquatic existence. It occupies the zone nearest the margin and by the growth of the rhizome extends into the water, often growing in water up to 5 ft. deep. The leaves then become floating leaves and the inflorescence stands erect above the water. The flowers are a deep pink.

Potamogeton javanicus Hasskarl is known from Florida Lake only, where it forms a dominant community on the east of the lake. The plant flowers from December to March. It has a few small floating leaves and several elongate submerged leaves.

Potamogeton richardii Solms-Laubach occurs in the large pan at Rietfontein, where it is dominant in the permanent ditches and in the surrounding parts of the pan. It also occurs as a small patch on the north side of Florida Lake. There are two forms of the plant, namely, a form with submerged and floating leaves, and a form entirely submerged, with no floating leaves. The submerged form occurs in very deep water and can be developed from the form with floating leaves, if the latter be grown in deeper water. The young plant has submerged leaves only until the shoot apex reaches the surface of the water, where it develops floating leaves.

D. *Reed Swamp Communities.*

The reed swamp may be divided into open and closed. The reed swamp communities are included with the aquatic communities since they exist largely under the same environmental conditions as the true aquatics. Florida and Geduld lakes have good examples of open and closed reed swamps.

Closed reed swamp. The communities of the closed reed swamp are zonally

arranged occupying zones near the margin and extending for some distance into the water. The plants which occur here are:

Phragmites communis Linn. which is a dominant both in the open and closed reed swamps. At Florida and Geduld lakes it occupies a zone extending for some distance into the lakes, often growing in water 4–5 ft. deep. The plant occurs both in fresh and stagnant waters. At Florida and Geduld the waters are fresh. In some of the pans around Lake Chrissie, which contain stagnant waters, it is found over almost the whole area of the pans. A pan about two miles north-east of Lake Chrissie was covered with *Phragmites communis* in May, 1928. Another pan west of Lake Chrissie, investigated at the same time, was not quite dry, having a stretch of about 20 ft. of water containing a zone of *Potamogeton pectinatus* Linn. and a zone of *Potamogeton richardii* Solms-Laubach, between the land and *Phragmites* zone. The drying up of these pans is probably caused by *Phragmites communis* which utilises most of the water, the supply of which is limited, being dependent on the rainfall. The plant also occurs in the marshes formed beyond the margins of the lakes, when the water-level falls and the swamp becomes a very wet marsh.

Typha australis Sch. and Thon. is found as a dominant in Florida and Geduld lakes.

Cyperus fastigiatus Rottboell occurs as a dominant on the north side of Geduld Lake.

Scirpus corymbosus Rottboell occurs as a dominant on the south-west side of Florida Lake, and on the north-east of Geduld Lake.

Open reed swamp. The open reed swamps include the members of the closed reed swamps as well as plants which belong to the free-floating community, and to the rooted and submerged communities, both with and without floating leaves. There are also zones of communities which are sub-terrestrial, but which, for certain periods, usually after torrential rainfall causing an extension of the water area, adapt themselves to an aquatic existence. These plants are zonally arranged according to their degree of adaptation to an aquatic existence.

Plants occurring in the open reed swamps, besides those mentioned as occurring in the closed reed swamp, are: *Juncus effusus* Linn., *J. oxycarpus* E. Meyer, *Juncus* spp., *Cyperus umbrosus* Nees, *C. macranthus* Boeck, *Polygonum limbatum* Meisn., *P. meisnerianum* Cham. and Schlecht., *P. serrulatum* Lag., *P. glutinosum* Meisner, *P. tomentosum* Willdenow, and *P. amphibium* Linn. This last species has already been mentioned in the communities of rooted plants with floating leaves.

Plankton and epiphytic algae occur in both the open and closed reed swamps.

Phot. 4. Aquatic vegetation in Florida Lake. The floating vegetation in right middle distance and left centre nearer the bank is *Limnanthemum thunbergianum* Grisebach. *Phragmites communis* L. and *Typha australis* Schum. and Thonn. are seen in right foreground. A tuft of *Scirpus corymbosus* Rottboell occurs in left foreground close to bank, and there are several others in the middle distance, further from the shore. The planted trees are *Salix babylonica* L. on the left, and *Eucalyptus* sp. on the further shore.

Phot. 5. Aquatic vegetation in Florida Lake. The reed swamp plants are mostly *Typha australis* with *Polygonum* sp. towards the right, showing characteristic inflorescences. The floating leaves are those of *Limnanthemum thunbergianum*.

WEINTROUB—AQUATIC AND SUB-AQUATIC VEGETATION OF THE
   WITWATERSRAND

III. Sub-aquatic Plant Communities.

The sub-aquatic communities include hemi-halophytic plants and marsh plants.

A. *Hemi-Halophytic Communities.*

These are represented by species of *Spergularia. Spergularia* sp.nov. (aff. *S. salina* J. and C. Presl) is found at the main pan at Brakpan and at Apex pan. At Brakpan it occurs in a swamp which contains a high percentage of salts in the soil and in the water. The salts on analysis were found to consist of chlorides, sulphates and carbonates, of sodium, calcium and magnesium.

Spergularia marginata Kitt. var.nov., is found on the north margin of Geduld Lake.

B. *Marsh Communities.*

There is no definite line of demarcation between marsh plants and land plants, but marsh plants tend to occur with their roots in soil containing much water.

Marsh plants are zonally arranged around the margin of the waters, the zones being determined by the amount of water present in the soil. Some marsh plants have the power of adapting themselves to an aquatic existence when they are submerged or nearly submerged. *Scirpus fluitans* Linn. develops long linear leaves when submerged. *Polygonum amphibium* Linn. develops floating leaves when growing in water. Some aquatic plants, namely, *Limnathemum thunbergianum* Grisebach and *Marsilia macrocarpa* Presl, can adapt themselves to existence as marsh plants.

On the west sides of Florida and Geduld lakes and on the east side of Canada Lake, there are marshes for the major portion of the year. At Florida and Geduld the marshes extend for some distance. The pans, on the other hand, when full of water have marshes for a short distance around their margins. In such marshes occur *Limosella tenuifolia* Wolf, *Lessertia* sp.nov. (at Avenue pan), *Cuscuta* sp.nov., *Trifolium* sp.nov., *Crotalaria distans* Bentham (at Avenue pan), *Aponogeton spathaceus* E. Meyer (at the large pan at Rietfontein), *Polygonum limbatum* Meisn., *P. tomentosum* Wildenow. With the end of the rainy season the pans at Brakpan and Rietfontein are converted into marshes. The whole pan, except the permanent pools and ditches, becomes a marsh which is covered with *Cynodon transvaalensis* Burtt Davy, *Limosella tenuifolia* Wolf, and marsh forms of *Marsilia macrocarpa* Presl. The Avenue pan when nearly dry has a bare covering of dark powdery mud. In the marshes around the lakes occur: *Cyperus isocladus* Kunth., *C. macranthus* Boeck, *Epilobium villosum* Curt., *Juncus effusus* Rottboell, *J. brevistylus* Buchen, *J. glaucus* Ehrh. var. *acutissimus* Buchen, *J. lomatophyllus* Spreng, *J. oxycarpus* E. Meyer, *Juncus* spp.nov., *Polygonum limbatum* Meisn., *P. meisnerianum* Cham. and Schlecht., *P. serrulatum* .Lag., *P. glandulosum* R. Br., *P. glutinosum*

Meisner var. *capense* Meisner, *Limosella tenuifolia* Wolf, *Limosella* sp., *Nasturtium officinale* R. Brown, *Pelargonium* sp., *Ranunculus sardous* Crantz, *R. meyeri* Harvey var. *transvaalensis, Scirpus macer* Boeck, and *Rumex glomeratus* Schreb.

IV. HABITAT CONDITIONS.

The habitat conditions which determine the distribution of the communities seem to be the physical and chemical nature of the waters, depth of water, movement of the water, aeration and the nature of the substratum.

Plankton occurs abundantly in the still and very slowly flowing waters, and is poor in quantity in the very swiftly flowing streams. The type and amount of plankton appears to be influenced by the chemical and physical properties of the waters.

The free-floating communities of Spermatophyta occur in still waters, such as the pans.

Rooted plants with floating leaves occur in clear waters in sheltered regions of the pans and lakes, and in backwaters of streams.

The communities of rooted plants entirely submerged occur in fairly deep waters on substrata of soft muds.

The reed swamps occur in very slowly flowing and still waters. When members which belong to the reed swamp occur in the streams, they do not form swamp communities.

The hemi-halophytic communities occur where there is a considerable proportion of salts in the soil, a very large percentage of the salts being sodium chloride.

In the case of the marsh plants, among the most important factors is the amount of available water in the soil.

A closer study of the habitat conditions must be made however in order to ascertain the correlation between the above factors and the distribution of the plant communities.

V. SUMMARY.

The area investigated extends from Florida, nine miles west of Johannesburg, to Brakpan, twenty-three miles east of this city.

The sheets of water may be classified as follows:

(1) Artificial dams, usually in connection with the gold mines, and, as a rule, of little botanical interest.

(2) Semi-natural lakes, made by the artificial damming up of natural streams. Florida Lake is the best known. Reed swamps occur, with the following plants locally dominant: *Typha australis* (very closely allied to *T. latifolia* and *T. angustifolia*), *Phragmites communis* (apparently the form of southern Europe), *Scirpus macrocarpus* (looking like *S. lacustris*), and *Cyperus fastigiatus*. Of plants with floating leaves, *Limnanthemum thunbergianum* (allied to *L. peltatum*) is abundant in Florida Lake. Submerged plants occur, such as
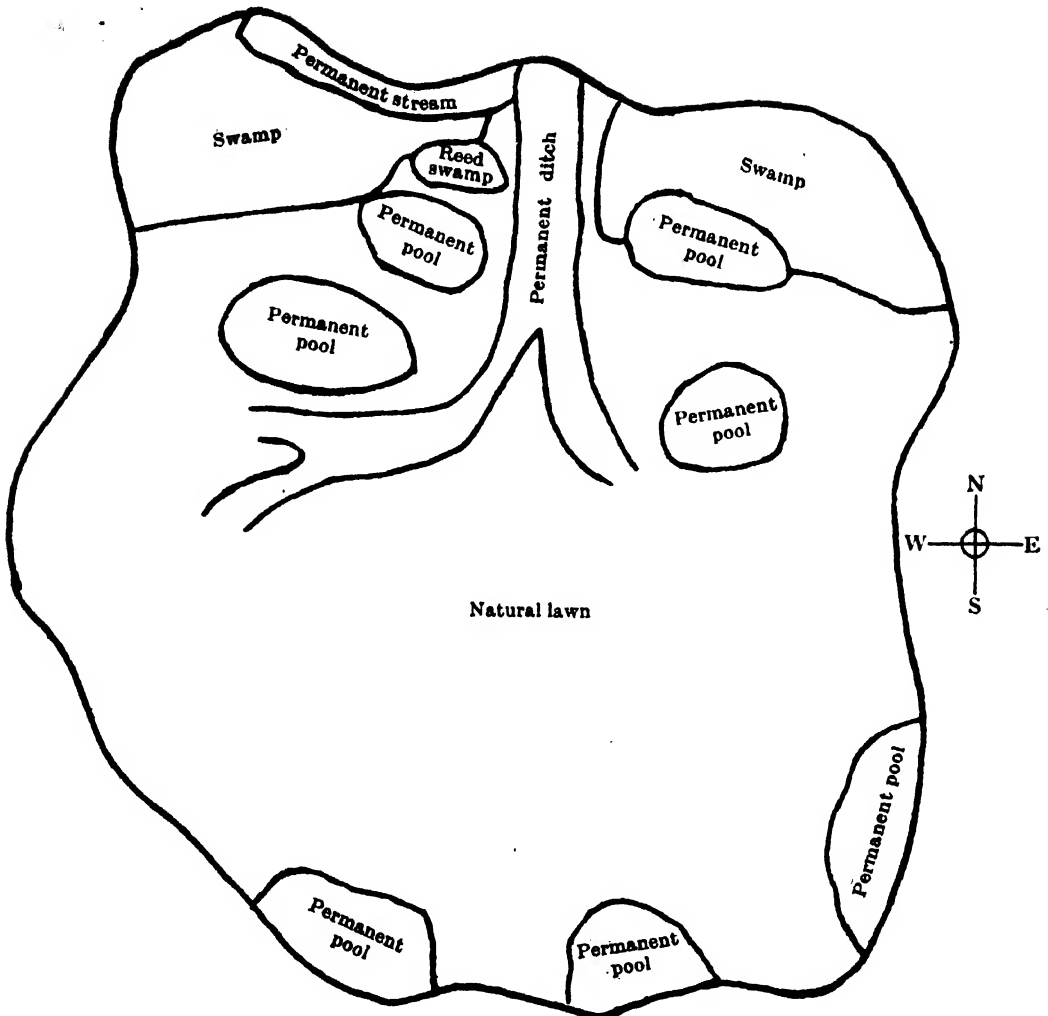
A. August 14, 1927: showing the physiographical features when the amount of water in the pan gives the maximum physiographical differentiation. The areas outlined in black—stream, ditch and pools, all artificial—are occupied by water. The rest of the pan, except the swamp areas at the north-west and north-east corners, is dry and forms a natural lawn covered with *Cynodon transvaalensis*.

LEGEND

✝✝✝✝✝ ✝✝✝✝✝ *Panicum coloratum* Linn.

Tragus sp.

Diplachne fusca.

Utricularia stellaris Linn.

Lemna gibba, L. and *L. minor.*

Zannichellia pedicellata Fries

Potamogeton pectinatus L.

Characeae (C and D).

Marsilia macrocarpa Presl

Lagarosiphon muscoides Harvey

Cyperus sp.

Typha australis Schum. and Thonn.

Spergularia sp. (aff. *S. salina* J. and C. Presl)

Cynodon transvaalensis Burtt Davy

Chara stachymorpha Gauterer

Chara fragilis Desvaux

Marsilia macrocarpa Presl (marsh form)

Polygonum sp.

Limosella tenuifolia Wolf

Panicum laevifolium Hack.

Potamogeton javanicus (with a few floating leaves), and *P. badius* (allied to *P. pusillus*), *Potamogeton* sp.nov. The margin is rich in marsh species, including *Juncus effusus*, *Juncus* spp., *Ranunculus sardous* (agg.), *R. meyeri* var. *transvaalensis*. *Nasturtium officinale*, and *Epilobium villosum* (aff. *E. hirsutum*). *Spergularia marginata* var.nov. occurs at the margin of Geduld Lake.

(3) Natural sheets of water, which are:

(*a*) Pans, or shallow depressions whose origin is in dispute. The pans are frequently dry in winter. They have a typical and characteristic marginal flora, with *Spergularia* sp.nov. (aff. *S. salina*), *Lessertia* sp.nov., *Cuscuta* sp.nov., and others. *Lemna minor*, *L. gibba*, and *Wolffia arrhiza* occur locally in the pans of the East Rand. *Potamogeton pectinatus* var. and *Zannichellia pedicellata* occur in Brakpan. The pans have a rich plankton, consisting chiefly of Copepods and Diatoms. *Volvox Rousseleti*, and *Hydrodictyon* (probably the recently described *H. indicum*) occur in Rietfontein pan. The pans have no streams flowing out of them, and consequently their mineral content is high, becoming almost supersaturated as the dry season approaches. Incrustations of salts are of common occurrence on the receding margins of the pans, as the water evaporates.

(*b*) Streams and their backwaters. The backwaters have the same flora as the lakes; and the stream banks yield the same plants as the margins of the lakes.

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NOTE.

While this paper was in the press the following contributions, dealing with the microflora of several localities discussed in this paper, were published.

Hutchinson, G. E., Pickford, G. E., and Schuurman, J. F. M. "A Contribution to the Hydrobiology of pans and other inland waters of South Africa." *Archiv für Hydrobiologie*, Bd. **24**, 1–154, 1932.

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STUDIES ON THE ECOLOGY OF RIVERS[1]

I. ON THE DISTRIBUTION OF MACROPHYTIC VEGETATION IN THE RIVERS OF BRITAIN

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(With Plates IX–XII and five Figures in the Text.)

CONTENTS.

I. INTRODUCTION.

STUDIES on the ecology of bodies of fresh water in this country are very few, and what has been done has been for the most part in lakes and ponds. West (**38** and **39**) has made a general ecological survey of the Scotch lochs, and Pearsall (**24**) has more recently given an account of the development of vegetation in the English lakes, but no other area of water seems to have been properly

[1] Portion of thesis approved for the degree of Doctor of Philosophy of the University of London.

investigated as regards the flowering plants, the mosses and the larger algae, though some work has appeared on the plankton.

A greater lack of data is found on the vegetation of running water. In *Types of British Vegetation* (Tansley (**34**)) the vegetation of rivers is divided into the subformations of slowly flowing and quickly flowing waters and only two pages are devoted to the subject. A preliminary account of the vegetation of the River Itchen has already appeared (Butcher (**7**)), while an account of the biology of the River Lark, dealing especially with its pollution by sugar-beet effluents (Butcher, Pentelow and Woodley (**11**)), contains a summary of the chief characters of the vegetation.

In this paper an attempt is made to correlate the various observations made by the author on British rivers, to summarise the various factors influencing the distribution of vegetation in moving waters, as contrasted with lakes and ponds, and to outline the various communities of plants in the same manner as has been done for woodland, heath, saltmarsh and mountain. This account deals with the flowering plants, mosses and larger algae, such as *Lemanea* and *Clado-phora*, which can be seen and recognised without the aid of a microscope. All these forms may be conveniently grouped together and called the macrophytic vegetation.

II. GENERAL ENVIRONMENT OF AQUATIC PLANTS.

The special conditions under which submerged aquatic plants live have been discussed by many workers, e.g. Arber (**2**), Glück (**15**), and need only be mentioned here.

(*a*) Water is superabundant, so that problems of water supply do not arise. Although there exists in water plants an upward current similar to the trans-piration current of land plants (Thoday and Sykes (**35**), Hochreutiner (**17**)) this is not produced by the evaporation from the leaf surface except in water plants with floating leaves, so that there is no danger of desiccation from this source.

(*b*) The intensity of the light reaching submerged plants is much less than that which falls on land plants and on the floating leaves of water plants. It has been shown by Regnard (**30**) that up to 60 per cent. of the light may be absorbed in passing through the first 2 m. of water. Oberdorfer (**23**), and Lönnerblad (**20**) give considerable information as to the amount of this ab-sorption, which is very large in turbid waters. There are very few waters that are perfectly clear, and the greater the amount of suspended matter the greater the light absorption, while the smaller the amount of light reaching the river bed the smaller the quantity of macrophytic vegetation.

(*c*) The temperature of bodies of water shows relatively small fluctua-tions, changes less rapidly and is for the most part lower than that of the air (Guppy (**16**)). Further, as increase in temperature cannot bring with it increase in evaporation from the plant surface, high temperatures are not attended by disastrous desiccation. Temperature governs the rate of decomposition of

organic matter in the water and in the substratum. The effect of temperature on the actual growth of aquatic vegetation need not be considered here.

(*d*) As indicated by Devaux (**14**), Arber (**2**) and others the actual quantities and proportions of the important gases, oxygen and carbon dioxide, present in water are very different from those in the atmosphere, as will be seen from the following figures of Winkler, and Bohr and Bock, taken from Bayley (**3**).

Comparing the relative percentages by volume of the three gases dissolved in water saturated at normal temperature and pressure, with those available in air we have:

	Water	Air
Oxygen	34·2	20·8
Nitrogen	63·4	79·1
CO_2	2·4	0·04

The actual amounts available as c.c. per litre of water and air respectively, are:

	Water	Air
Oxygen	10·24	208·0
Nitrogen	18·99	791·0
CO_2	0·68	4·0

Obviously both oxygen and carbon dioxide are available in much smaller quantities for a submerged water plant, but the diminution in carbon dioxide is proportionately much less. And since these figures only relate to dissolved CO_2 there is a further large reserve in many waters in the form of dissolved bicarbonates. But the rate of diffusion of gases in water is an important complicating factor, and the results of Brown (**6**) and later of Butcher, Pentelow and Woodley (**10**) seem to indicate that diffusion is comparatively slow.

Further, as shown by Butcher, Pentelow and Woodley (**9**) in studies on the River Lark, the variation of these gases within a single day may be enormous in water containing an abundance of green plants. These results, confirmed by Hubalt (**18**), although obtained in a river, apply also to bodies of still water as indicated by Morren (**22**), who records big variation of oxygen and CO_2 in an aquarium, by Chambers (**12**) who records variations of oxygen between 240 and 40 per cent. saturation, and finally by Cowles and Schwitalla (**13**) and by Saunders (**33**), who describe variations in pH and attribute them to photosynthesis. More recently Wehrle (**37**), working on still waters of various types whose mean pH values were from 3·5 to 7·5, has produced evidence of diurnal variations. The waters of low pH (between 3 and 4) show very little variation, while in waters of higher pH his curves are similar to those recorded by Butcher, Pentelow and Woodley, the results of whose work may be summarised here.

(1) During the day oxygen is produced in large amounts by photosynthesis.

(2) This oxygen does not immediately return to the atmosphere but remains as a supersaturated solution in the water.

(3) The highest supersaturation figures were obtained when algae were most abundant, and it is suggested that this phenomenon is correlated with

the size of the gas bubble exuded from the plant surface. This bubble must be
very minute in the case of an algal cell or diatom and comparatively large
from the tissues of a phanerogam.
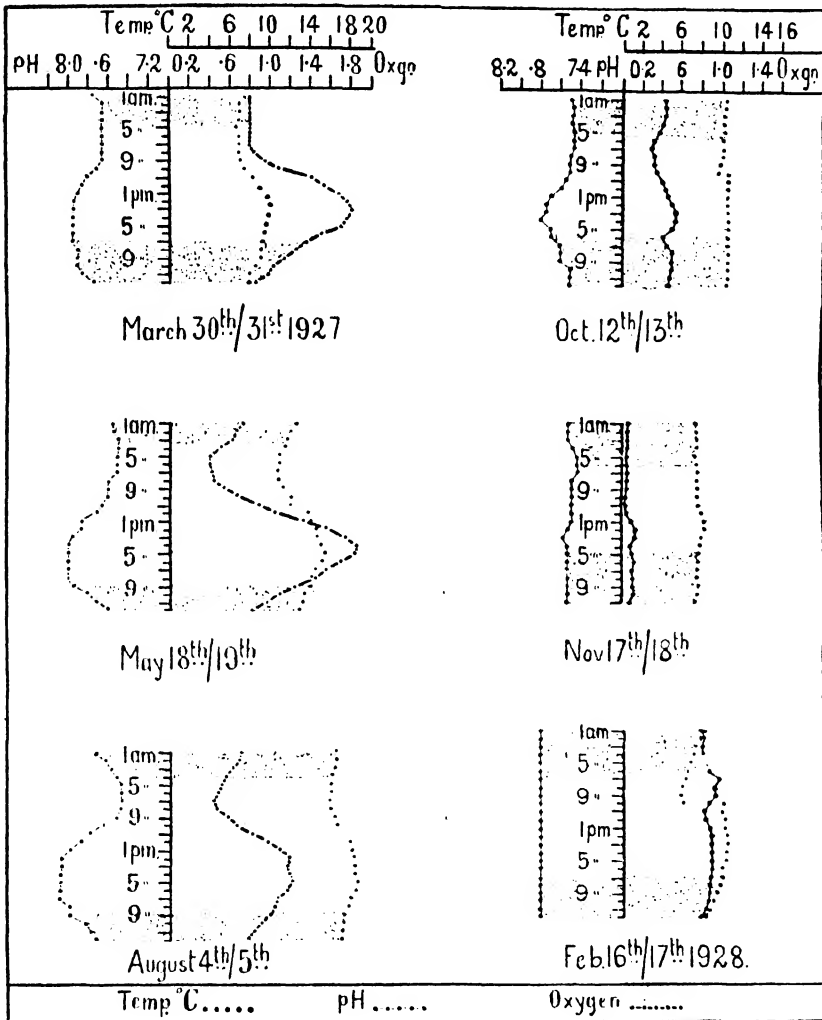
Variation of Oxygen, pH and Temperature at Icklingham.

FIG. 1. Diurnal variation of dissolved O_2, pH and temperature in the River Lark.
(Reproduced from Pentelow, Butcher and Woodley (11).)[1]

(4) Much of the oxygen produced during the day is used up by the respira-
tion of plants and animals and by the decay of organic matter in the mud
during the night, and CO_2 is then produced in large quantities, resulting in a
considerable fall in the pH value of the water.

(5) Shortage of free CO_2 during the active assimilating period is made good
by the absorption of the "half-bound" CO_2 in bicarbonates which are present

[1] Figs. 1, 3, 5 and Phot. 2 and 4 are reproduced by permission of the Controller of H.M.
Stationery Office.

in large quantities in many streams; only rarely is CO_2 a limiting factor (see also Wiebe (**41**)). It has recently been established that normal carbonate is present in the Tees at times of great assimilative activity[1].

(6) When water is subsaturated in respect of oxygen the deficiency is only made good very slowly by diffusion from the atmosphere and the rate of diffusion is least in still water (cf. Birge and Juday (**4**), Alsterberg (**1**), etc.). Fig. 1 shows some typical examples of this variation.

(e) *Mineral salts*. There are two sources from which aquatic plants may obtain mineral salts: from salts in solution in the water and from the substratum. Rooted aquatic plants, although wholly submerged, obtain their mineral salts from the substratum and not from the surrounding water. Pond (**29**) showed this to be definitely the case with *Ranunculus trichophyllus*, *Myriophyllum spicatum*, *Potamogeton obtusifolius* and *Vallisneria spiralis*, which were found to grow better with a substratum of soil than with one of clean, washed sand. On the other hand floating or drifting plants such as *Ceratophyllum* and *Lemna*, besides the algae, obtain their mineral salts from the surrounding water. Variations in the dissolved salts in the water will therefore be of little consequence to rooted aquatics, but deposition of silt and suspended matter from the water and the composition of these silts (whether containing much decaying organic matter or not) or, on the contrary, the removal of the substratum by waves or currents, are among the chief factors that govern the quantity and variety of macrophytic vegetation both in still and flowing water.

III. Particular characteristics of a river habitat.

The fundamental difference between a river habitat and that of a pond, lake or bog, lies in the existence of a current. The water is always moving in one direction and there is a continuous supply of dissolved and suspended mineral and organic matter brought in by the drainage water. Part of this supply is temporarily trapped as sediment or by the plants and animals directly, but it all ultimately reaches the sea and the loss is made good by a further supply. Without this the river would become for the most part barren, as the deposited silts supply to a large extent the mineral salts of the rooted plants and the dissolved matter supplies the algae.

It may be said, generally, that the effect of flowing water is to reduce the amount of variation in most of the conditions outlined above. Risk of death due to the failure of water supply is even less than in ponds, and the temperatures show less fluctuation and tend to change more slowly even than in still water.

The quantity and quality of the light falling on the river bed changes rapidly in relation to the rainfall. A heavy shower or storm raises the level of the water and leads to the introduction of quantities of silt. The resulting turbidity, however, lasts for only a short time after the rain has ceased.

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[1] I am indebted to my colleague, Mr J. Longwell, for this information.

The influence of moving water on the O_2 and CO_2 relations is to reduce the amount of daily variations, and this effect will be proportional to the turbulence and speed of the current. Its extent must not, however, be over-estimated, since even in the River Tees, with a current of 6000 yards an hour, considerable variation in O_2 and CO_2 can occur in the presence of a sufficient abundance of plants (e.g. *Cladophora*). Rivers full of green plants, whatever their speed, will show these variations, but as light is the limiting factor, a flood bringing in quantities of turbid water will considerably reduce this diurnal fluctuation. On some days therefore there will be little variation, on other days a great deal.

Effect of current on the stability of the substratum.

Most important of all, however, is the effect of the current in a river on the river bed, which is both the rooting substratum of the large plants and the source of their mineral salts. All plants that are to remain permanently in a river must be rooted or attached in some way, so that for them stability of the bed is of the greatest importance. A river bed consisting of stones that are being continually turned over by current and eddies will have no rooted vegetation and no animals (Percival and Whitehead (**27**)), as they will never get a chance to "settle down." Similarly with a bed of sand or gravel sudden floods will wash away the sand together with the plants rooted in it.

The strength of the current primarily determines the general nature of the river bed as the following table taken from Minnikin (**21**) shows:

Velocity of current			Nature of river bed
Greater than	4·0 ft. per sec.		Rocks
„	3·0	„	Heavy shingle
„	2·0	„	Light shingle
„	1·0	„	Light gravel
„	0·67	„	Sand
„	0·42	„	Silt
Less than	0·42	„	Mud and alluvial deposits

As, however, the velocity of the current is not constant the bed of the river will be unstable. A flood will always tend to shift the smaller particles at a given place, and when the water subsides new particles brought in from the surrounding land, or from other parts of the stream, will again be deposited. It is obvious, therefore, that a river bed is very unstable as compared with the bottom of a lake or pond, and the greater and more frequent the changes in water-level in a given part of a river the less chance there is for plants to become permanently rooted there. Rain washes into a river silt and organic detritus, the amount and nature of which depends on the nature of the land adjacent to its banks; it will be least in mountainous districts, much more considerable in agricultural districts and greatest in densely populated regions. In the last also, sewage, more or less purified, ultimately reaches the river and will tend to increase organic matter. This increase is often very considerable, since a great many sewage purification works have not the capacity to deal with the increased flow at times of heavy rainfall, and the crude sewage over-

flows straight into the watercourse and later into a river. This organic detritus is light and will therefore be deposited chiefly among the finer muds and silts, making these deposits more fertile. In addition to deposition however, precipitation and absorption of colloidal organic matter also takes place (Butcher (8)), and this precipitation will again be greatest among the finer muds. The irregularities of a river bed produce local eddies leading to local deposition of finer particles, whilst much silt is arrested by dense growths of macrophytes as well as by mats of filamentous algae and "sewage fungus" when these are present in the river in sufficient quantity.

A good example of this trapping of silt is seen at Low Middleton on the River Tees. In May, 1930, a wire was fixed across the river just below some patches of *Ranunculus fluitans*, and the vertical distance between a fixed mark on the wire and the surface of the river bed was 37 cm. In September, 1930, the plants had grown downstream over the wire and the vertical distance had decreased to 15 cm., due almost entirely to the collecting of silt among the patches of macrophytic vegetation.

Mechanical effect of current.

In addition to, and more or less complementary with, the eroding effect, there is the continual stress and strain the current exerts on the plants in the water, tending always to sweep them downstream. It is evident, therefore, that only rooted plants can remain stationary and all vegetation will spread downstream. There must be some means of the vegetation becoming again established upstream, otherwise the river would become devoid of plants, a tendency which can be seen near the source of any river. Obviously this re-establishment may be brought about partly by air-borne spores or other disseminules from ponds and marshes that only overflow occasionally, or from amphibious plants near the banks of the river.

The greater the current the greater the pull, so that plants in swift rivers must either be possessed of strong stems and leaves and efficient rooting systems (e.g. *Ranunculus fluitans*) or exhibit a close cushion-like growth that offers little resistance to the current (e.g. *Eurhynchium rusciforme*). The filamentous algae, like *Cladophora* and *Batrachospermum*, are in a rather different category, since parts of the filaments must be continually torn away, although the loss is rapidly made good by further growth.

Floods.

Periodically the amount of water in any river is greatly increased by high rainfall. The resulting augmented strength of the current will act adversely on the vegetation. As pointed out above, the substratum, even if of stones and boulders, will be moved, and much of the vegetation insecurely anchored in gravel and among the stones will be torn to pieces or rooted up by the swirling waters. This is well illustrated by the quadrat studies in the River Itchen (see

p. 82). The greater the addition to the volume of the water, the greater the damage done. From these considerations it is obvious that for the successful establishment and maintenance of a colony of plants in a river the same conditions must obtain for a considerable period, whereas large fluctuations may result in the washing away of entire growths in one or two days. Even in portions of a river with a very fast current plants can obtain a hold and, when once established, will collect silt and organic detritus around themselves, this silt in its turn enabling the colonies to increase their area and new plants to arise in the shelter of the tufts. A simple increase in volume of the water in a river need not mean that damage is done, for in some cases, especially in deep rivers, there is comparatively little increase in current in the lower layers, i.e. directly above colonies of plants rooted on the bottom.

General review of river conditions.

Given therefore similar chemical and physical conditions, such as usually obtain for long stretches of a river, the velocity of the current is the most important factor. The plant communities should therefore vary according to the strength of the current and consequently according to the nature of the river bed. These communities can conveniently be summarised as follows:

(a) *Current: very fast. Nature of bed: rocks.* The vegetation will be sparse owing to lack of organic silt and insufficiency of rooting places. The growth will take the form of small cushions, tufts or crusts, e g. mosses, filamentous algae, thalloid algae and liverworts.

(b) *Current: fast. Nature of bed: stony.* The vegetation will consist partly of the same types as under (a) and partly of plants possessing strong stems with small leaves (e.g. *Sium erectum, Myriophyllum spicatum*), tough and woody rhizomes, or roots capable of forming a lattice-work among the stones (e.g. *Potamogeton densus*). If the colonies become large, silt and organic detritus is trapped by them, and plants of the silted community can then establish themselves.

(c) *Current: moderate. Nature of bed: gravel.* The vegetation will probably be of the same character as the last, but more varied and more abundant as conditions are more favourable.

(d) *Current: slow. Nature of bed: sandy.* This is a rather loose substratum and the vegetation will be sparse except under very uniform conditions, or until the bed becomes consolidated by plant growth. The characteristic plants will have fibrous roots (e.g. *Callitriche stagnalis*) or matted rhizomes (e.g. *Sparganium simplex*) and weak or strong stems; but above all they will exhibit a rapid growth that will enable them quickly to push through a covering layer of sand and silt. Mosses and attached algae (*Cladophora* and *Batrachospermum*) will be absent save on piles or embankments, as there is no other firm substratum to which they can attach themselves. This is shown by Richards (31) to be the case in the streams of Middlesex, including the Thames.

(*e*) *Current: very slow. Nature of bed: silt.* The vegetation will be abundant and of the same character as under (*d*). The dominant plants will be those with small and very abundant roots, forming mats or tufts and capable of withstanding continual smothering with silt or sand (e.g. *Elodea canadensis*).

(*f*) *Current: negligible. Nature of bed: mud.* The vegetation will approximate to that of a pond or the shore of a lake. Erect reeds will be present and plants similar to those under (*e*) will live among them. The underground parts will be composed either of fibrous roots or of thick rhizomes.

The effect of sudden heavy floods will in general be to reduce the quantity of the vegetation and cause it to approximate more closely to the communities of the swifter water above. Equable conditions with few floods will cause the vegetation to change in the direction of that characteristic of the community in the slow-flowing water below. The effect of turbid or deep water will be to diminish the quantity of vegetation, because of the considerable reduction in light intensity (cf. Pearsall (**25**)).

The different communities of plants found on the various types of river bed have been given special names in my papers on the Lark and Itchen, and this terminology can now be widened as follows:

Type of bed	Community
Boulders	Torrential
Large stones	Non-silted
Gravel | Sand	Partly silted
Silt	Silted
Mud	Littoral

When different rivers on different geological formations are considered it is evident also that anything that changes the chemical composition of the water and therefore of the substratum will also change the vegetation to a greater or less extent.

General review of English rivers.

As pointed out above, the essential character of a river is that the water is continually moving towards the sea except where it comes under the influence of tides, but beyond this there is no general feature and many differences are to be found.

Considering first the origin or source of a stream three different types can be distinguished:

Group 1. Those rising in high hills or mountains, e.g. Tees.

Group 2. Those rising from springs and from the drainage of fairly low-lying lands, e.g. Lark, Itchen and Chess.

Group 3. Those that rise in low-lying marsh or fenland, e.g. Little Ouse, Waveney.

Those in the first group comprise many of the rivers in Northern England and Wales and are characterised by the swiftness of the current in many parts of the course, the presence of natural waterfalls or cascades and the incidence of very heavy floods due to the large area of the gathering grounds, the high and

sudden rainfalls, the steepness of slope, and the comparative impermeability of the rocks which involves a large amount of surface drainage. Sudden increases in level of from 5 to 12 ft. are not infrequent in some of these streams. Those in the second group comprise most of the streams of Southern England and many of the small feeders of the larger rivers. The current is dependent on the elevation of the source as compared with the length of the stream, but it is never torrential and, what is more important, floods are inconsiderable or gradual—a rise of 3 ft. being a great deal—as there is comparatively little surface drainage in contrast to sub-surface drainage. Those in the third group are rare. They are slow-flowing and contain a fairly high amount of dissolved salts derived from the marshes and fields in which they rise.

These rivers may further be classified according to the nature of the substratum and the chemical composition of the water. The usual classification is calcareous streams and non-calcareous streams, but this can be further extended as follows:

(a) *Non-calcareous and highly acid* waters have a hardness figure of less than 2·0 parts per 100,000 $CaCO_3$. Rivers of this group are rare. That colouring of the water by peat is no indication of acidity is shown by the River Tees, whose waters, even when very brown, have a pH of 7·0–7·5. The best examples of streams of this first type that I have observed are (1) the New Forest streams with a pH of about 6·5 and belonging to group 3 above (the streams rising from lowland bogs), (2) the streams in Ross and Sutherland belonging to group 1 above (the highland streams).

(b) *Slightly calcareous and almost neutral* waters have a hardness figure between 2·0 and 10·0 parts per 100,000 $CaCO_3$ and are not rare. I have investigated no good samples in groups 2 and 3, but the Tees is a good example of group 1.

(c) *Moderately calcareous and alkaline* waters have a hardness figure between 10 and 20 parts per 100,000 $CaCO_3$ and are represented by the River Tern in group 2 and the lower Tees after the confluence of the Skerne in group 1.

(d) *Highly calcareous and alkaline* waters with a total hardness figure above 20 parts per 100,000 $CaCO_3$ are frequent. The Little Ouse is an example of group 3, the Itchen, Lark, Chess and Skerne of group 2 and the Wharfe of group 1.

All rivers are modified by the inflow of organic matter as they pass agricultural land and large towns, a process which may be termed pollution or better still eutrophication. The above groups can thus be again subdivided according to their organic content into those which are very rich, poor, or very poor in organic substances.

As a river flows towards the sea there is a continual increase in the volume of water, in size and depth, and in the amount of suspended matter. When a river becomes so deep and so turbid that there is not sufficient light penetrating to the river bed to admit the growth of macrophytic vegetation, an entirely

different type of river results which does not enter into the scope of the present paper. Examples are afforded by the Warwickshire Avon and the lower parts of the Thames, Trent and Severn.

Development and alteration of rivers.

There are thus at least twenty-four possible variants in the physical and chemical characters of a river and these are further complicated by the alteration due to man, resulting from the fuller use of rivers for (1) drainage, (2) water supply, (3) water power, (4) navigation, (5) as a fishery, and (6) as a channel for the taking of refuse.

Drainage. Probably the most important function of a river is that it should act as a drainage system, conveying away to the sea the rain water that falls on the land. The swift rivers, where periodic increases in water are large, fulfil this function well, but the streams of the lowlands (e.g. the fenland rivers) are less efficient and therefore have to be dredged and cleared out at times, so that water plants are periodically removed; also sluices are often built and new channels are cut. An excellent illustration of changes brought about by drainage works is seen in the Ouse at Earith, Hunts., where the Bedford rivers (artificial canals) take away most of the water that it must have contained in former times.

Water supply. River waters are also used as a source of domestic water supply. The purest water is most in demand, so the supplies are usually taken near the source of the river. The use of water from springs diminishes the volume in the upper part of the river, while the construction of collecting reservoirs has the same effect and reduces the frequency of the floods. When a service reservoir is built the volume and rate of flow of the stream below it becomes almost constant throughout the year. Such alteration is well illustrated in the River Colne (Herts.), where the diminished volume of water has resulted in the silting up of large portions of the upper reaches and has changed the vegetation from that of a river to that of a pond or lagoon.

Water power. From the earliest times rivers have been used as a source of power to turn machinery and grind corn. To enable this to be done a dam is built across the stream to hold back the water. This causes a slowing down of the currents for a certain distance above the dam. Examples of some of the resulting changes are to be seen in the Itchen (Butcher (7)) and in the Lark (Butcher, Pentelow and Woodley (11)).

Navigation. Navigation has taken place on suitable portions of rivers from time immemorial, but there have been continual efforts to make other rivers navigable (e.g. the River Lark whose navigation act is dated 1700), and these efforts reached their climax at the end of the eighteenth century when so many of our canals were constructed. This interference with natural rivers has brought about a very marked change in their physical and biological condition owing to slowing down of the current, widening of the river bed and the cutting

of new channels. Excellent examples of this are the River Gade and the Grand Junction Canal, the River Gipping and the River Lark.

Fish production. In order to increase the number and size of the fish in a stream, alterations are made such as building small dams, regular cutting of weeds and digging out new channels. These are rarely large enough to effect any marked change.

Refuse disposal. Finally, man sees in a river a convenient means of disposing of his refuse and of his waste water. Where the density of population is very small and the volume of water great, little harm is done, but during the last 150 years the population has greatly increased and England has changed from a rural into an industrial country. Domestic and trade refuse has been emptied into the rivers in ever-increasing quantity, so that in course of time many became foul-smelling and the bearers of disease. In the middle of the last century there came the inevitable reaction against this pollution, and the Royal Sewage Commission was formed, whose reports (**32**) have appeared from time to time; many sewage disposal works have been erected and an improvement in many of our streams is noticeable (see Royal Sewage Commission (**32**)). But, as industries and populations grow quicker than methods for purification of the waste waters, fresh cases of pollution are continually arising, and bring with them profound changes in the biology and ecology of the streams (see particularly Butcher (**11** *a*)).

IV. CONSIDERATION OF EXAMPLES OF THE MAIN TYPES OF RIVERS.

This section shows how the more characteristic plant communities of certain streams conform to the general principles outlined above. Not all the diverse kinds of rivers mentioned have been properly examined, but there are sufficient data to show a definite relation between certain physical and chemical characters of a stream and its vegetation.

A. *Non-calcareous and acid rivers.*

From low-lying marshland.

The New Forest streams. These streams rise in bogs amid woodland and none are of very large size. They are usually clear and exhibit slow-flowing and freely flowing portions, while the water is poor in mineral salts. The vegetation[1] is as follows:

(*a*) *In the stony and rapid-flowing portions:*

Ranunculus pseudo-fluitans	d.	Callitriche intermedia	f.
Myriophyllum alterniflorum	f.	Potamogeton pusillus	r.
Potamogeton alpinus	o.		

(*b*) *In the slow-flowing portions:*

Myriophyllum alterniflorum	f.	Potamogeton alpinus	f.
Potamogeton polygonifolius	f.	Montia fontana	o.
Myosotis repens	o.	Sparganium simplex	o.
Nitella opaca	o.	Apium inundatum	r.

[1] In this paper the notation indicating the frequency of the various plants is as follows: d. dominant, c.d. co-dominant, s.d. sub-dominant, a. abundant, f. frequent, o. occasional, r. rare.

(c) *In the silted stretches.* These are the only places where the vegetation is at all plentiful, the chief plants being:

Potamogeton polygonifolius	d.	Callitriche stagnalis	a.
P. alpinus	f.	Ranunculus Lenormandi	f.
Scirpus fluitans	f.	Juncus supinus	f.
Nymphaea lutea	f.	Callitriche intermedia	r.

The sparseness of the vegetation resembles that of the non-calcareous streams in the west of England and in Surrey. None of these latter have been thoroughly investigated, but in the River Leven, Lancashire, for example, the dominant plants are:

(a) In the swiftest portions among stones: *Ranunculus fluitans, Myriophyllum spicatum.*

(b) In the slower flowing portions on gravel: *Potamogeton nitens, Myriophyllum spicatum.*

(c) In the silted stretches: *Callitriche intermedia.*

Lake Windermere, whose waters form the river, has a pH of 7·2 and a $CaCO_3$ content of 0·88 parts per 100,000.

The River Mole (Surrey). In this stream *Potamogeton heterophyllus* is common in sandy places, while *P. Friesii* and *P. obtusifolius* are the commonest plants in the muddy stretches.

B. *Very slightly calcareous but alkaline rivers.*

Rising in mountainous districts.

The River Tees rises on Cross Fell and has an acid water (pH about 5·0 from one observation[1]), but within a very short distance from its source it comes into contact with outcrops of limestone and the pH is almost immediately raised to about 7·5, this value being maintained for the rest of its course. The calcium content remains low (about 5·5 parts per 100,000 $CaCO_3$) until after the junction with the Skerne. The river is one of the swiftest in England and floods are numerous and extensive, a rise of 3 or 4 ft. within 24 hours is frequent. As is to be expected on the basis of the considerations put forward in section III the river is for the most part devoid of phanerogams and the only macrophytic vegetation consists of mosses and larger algae, the commonest of which are:

Fontinalis antipyretica	a.	Eurhynchium rusciforme	a.
Lemanea fluviatilis	a.	Cinclodotus fontinaloides	o.
L. mammillosa	o.	Grimmia fontinaloides	r.
Amblystegium fluviatile	o.		

Even in the comparatively slow-flowing stretches macrophytic vegetation is scarce. One reason for this lies in the fact that the bed consists for the most part of solid rock, and some stones and sand. The latter form a very unstable substratum during the frequent floods, and in this no plants can retain a hold

[1] Teste J. **Longwell.**

Phot. 1. Non-silted association in the River Tees at Neasham—*Ranunculus fluitans* dominant.

Phot. 2. Silted association in River Lark. Dominant plants are *Sagittaria sagittifolia* and *Sparganium simplex*.

BUTCHER—Studies on the Ecology of Rivers: I. Distribution of Macrophytic Vegetation in the Rivers of Britain

for long. On the surface of solid rocks only the cushion-like mosses and algae can anchor themselves securely enough to resist the frequent scouring by floods.

An exception is found above Cauldron Snout in a pond-like expansion of the river bed known as the weel. Here, owing to the much smaller volume of water and the smaller current, flooding does not interfere to any great extent with the river bed, which consists of sand and gravel. The plants growing here are:

Potamogeton alpinus	f.	Sparganium simplex	f.
Callitriche intermedia	o.	S. affine	o.
Fontinalis antipyretica	r.	Equisetum palustre	o.

C. *Moderately calcareous rivers.*

Rising in mountainous regions.

The River Tees. Below the confluence of the Skerne the calcium content of the Tees increases to about 12·0 parts per 100,000 $CaCO_3$, and the river may be considered as a representative of the moderately calcareous type rising from mountains. In this portion the swiftest stretches still have a bed of stones and boulders and here the vegetation is sparse and similar to that found in the upper reaches, viz.:

Fontinalis antipyretica	f.	Eurhynchium rusciforme	f.
Grimmia fontinaloides	r.	Amblystegium fluviatile	r.

and at times:

Cladophora glomerata	Lemanea mammillosa

In the somewhat slower flowing stretches, where the bed is composed of large and small stones, the vegetation consists of:

Ranunculus fluitans	d.	Potamogeton interruptus	s.d.
Fontinalis antipyretica	f.	Eurhynchium rusciforme	r.

(see Pl. IX, phot. 1).

Where the current is of medium strength the river bed consists of gravel and the vegetation is sparse, but when once established the plants collect a large amount of sand and are thus able to secure a hold. The plants found in such places are:

Ranunculus fluitans	d.	Potamogeton interruptus	s.d.
Myriophyllum spicatum	r.	P. crispus	f.
Elodea canadensis	r.	P. pusillus	r.
Nitella opaca	r.	P. perfoliatus	r.

Beds of fine mud and silt are only found as small patches near the banks and there are no extensive stretches of silt that could support a silted community. On the small areas of silt near the banks there occur:

Elodea canadensis	f.	Potamogeton crispus	f.
Nitella opaca	r.	Callitriche stagnalis	o.

The River Wharfe (Yorkshire). Another example of a moderately calcareous river rising among the hills, but with a slower flow than the Tees, is the River Wharfe, which rises on the Millstone Grit but very soon (at Kettlewell) flows over mountain limestone. Lower down, for the sixteen-mile stretch from Bolton

Abbey to Harewood, the underlying substratum is millstone grit, after which it is once more calcareous (Magnesian Limestone). Parts of the river are very swift, and it is subject to fairly considerable and sudden rises in water-level. Vegetation is sparse, particularly above Ilkley, and for the most part consists of mosses. The calcium content of the water is about 12·0 parts per 100,000 $CaCO_3$ (40). This river becomes more calcareous in the lower part of its course. Following are the chief plants:

(a) *Among rocks and boulders in the upper portion:*

Fontinalis antipyretica	f.	Eurhynchium rusciforme	f.
Amblystegium fluviatile	r.	Cinclodotus fontinaloides	r.

(b) *In the swift portions lower down among large stones:*

Ranunculus fluitans	d.	Potamogeton densus	f.
Fontinalis antipyretica	f.	Eurhynchium rusciforme	f.
Lemanea spp.	f.	Sium erectum	o.
Batrachospermum spp.	o.	Cinclodotus fontinaloides	o.

(c) *In the slower portions among gravel:*

Potamogeton perfoliatus	d.	Sparganium simplex	f.
Ranunculus fluitans	f.	Chara vulgaris	r.
Elodea canadensis	r.	Callitriche stagnalis	r.

From low hills.

The River Tern (*Shropshire*), with a pH of about 8·0 and a calcium content of 18·0 parts per 100,000 $CaCO_3$, can be taken as an example of a moderately calcareous river of this type. There are several others in various parts of England (e.g. the Tame in Warwickshire).

The Tern is not liable to sudden floods, though the water rises gradually and to a considerable height during the wet seasons. The water is usually turbid and this has the effect of reducing the amount of vegetation, especially in the slow-flowing and deep portions.

(a) *In the fastest stretches which have a bed of coarse gravel:*

Ranunculus fluitans	s.d.	Myriophyllum spicatum	s.d.

(b) *In the medium stretches with a bed of fine gravel:*

Sparganium simplex	d.	Sagittaria sagittifolia	f.
Polygonium amphibium	f.	Scirpus lacustris	f.
Callitriche stagnalis	f.	Elodea canadensis	o.
Potamogeton crispus	o.	Potamogeton pectinatus	o.
P. perfoliatus	o.		

(c) *In the slow muddy stretches.* Submerged vegetation is almost absent. This may be due, as pointed out above, to (1) the unstable substratum of sand and mud, (2) the low light intensity resulting from the frequent turbidity of the water, or (3) the "exhaustion" of the substratum. A certain number of erect plants however grow near the banks forming a littoral zone. These are:

Sparganium erectum	d.	Scirpus lacustris	s.d.
Sagittaria sagittifolia	f.	Butomus umbellatus	f.
Myosotis palustris	f.	Nasturtium amphibium	o.
Alisma Plantago	o.	Typha latifolia	o

D. *Highly calcareous rivers.*

Rising among mountains.

The River Dove (Derbyshire). No river of this type has been thoroughly investigated, but the Derbyshire streams are very good examples and particularly the River Dove. These rivers are among the cleanest and best of trout streams. They are in their upper reaches subject to moderate floods which tend to reduce the amount of vegetation, so that, unlike the chalk streams of Southern England, there is no need to keep down the weeds by cutting.

(*a*) *In the fastest stretches* of the Dove which lie in the upper reaches between Axe Edge and Hulme End the river bed is almost bare of flowering plants but some mosses occur, viz.

Fontinalis antipyretica	f.	Eurhynchium rusciforme	f.
Cinclodotus fontinaloides	o.	Amblystegium fluviatile	r.

(*b*) *In the fast-flowing stony stretches* from Hartington downwards there occur:

Ranunculus fluitans	d.	Sium erectum	a.
Potamogeton densus	o.	Apium nodiflorum	r.
Veronica Anagallis	o.	Myosotis palustris	r.

(*c*) *In the gravelly stretches:*

Sparganium simplex	a.	Ranunculus fluitans	a.
Mimulus Langsdorffii	o.	Potamogeton perfoliatus	f.
Potamogeton densus	r.	P. crispus	r.

(*d*) *In the very slowest stretches* with a bed of fine mud there can usually be found:

Callitriche stagnalis	a.	Elodea canadensis	f.

The vegetation has, however, not been examined in detail below Hanging Bridge, where silted stretches are more frequent. These silted parts tend to have a much sparser vegetation than the stony and gravelly stretches, and this may again be due to any of the factors mentioned on p. 85, viz. unstable substratum or exhaustion. This type of river differs from the next two types in the presence of a torrential community composed chiefly of mosses, also in the absence of a well-marked silted community and in the comparative abundance of mosses throughout.

Rising among hills and from springs.

This type of stream is extremely common in Southern England and there are several good examples in the north, e.g. The Hull (Yorkshire).

The River Itchen (Hampshire) is a typical instance of such streams, which, like those just mentioned, are very good trout waters. The pH of the Itchen is between 7·0 and 8·0 and the calcium content 23·0 parts per 100,000 $CaCO_3$. The water is very clear. The average rate of the current is somewhat greater than that in the group of rivers last considered, but as with them, water-level

and current remain relatively constant so that vegetation is abundant. The vegetation of the Itchen is as follows:

(a) In the fastest stretches:

Ranunculus pseudo-fluitans	d.	Apium nodiflorum	s.d.
Sium erectum	s.d.	Potamogeton densus	a.
Fontinalis antipyretica	a.	Nasturtium afficinale	a.
Veronica Anagallis	f.	Mimulus Langsdorffii	r.
Oenanthe fluviatilis	r.	Cladophora sp.	r.

(b) In the gravelly stretches with medium current:

Hippuris vulgaris	s.d.	Sparganium simplex	s.d.
Oenanthe fluviatilis	a.	Scirpus lacustris	a.
Elodea canadensis	f.	Callitriche stagnalis	f.
Potamogeton densus	f.	Potamogeton crispus	r.
Lemna trisulca	r.	Ranunculus fluitans	r.
Ranunculus pseudo-fluitans	r.	Apium nodiflorum	r.
Sium erectum	r.	Typha latifolia	r.

(c) In the slow-flowing stretches:

Elodea canadensis	d.	Callitriche stagnalis	s.d.
Hippuris vulgaris	a.	Sparganium simplex	a.
Oenanthe fluviatilis	f.	Potamogeton pusillus	f.
Potamogeton crispus	r.	P. densus	r.
Ranunculus fluitans	r.	Vaucheria sp.	r.

It will be noted that these communities are very similar to those of the Lark (see p. 75), save that the silted community is not so well represented owing to the fact that there is very little fine silt and mud in the Itchen. In other streams of this type (e.g. the Gade and the Ver (Hertfordshire) and the Skerne (Durham)) the same communities are recognisable, with either *Ranunculus fluitans* or *R. pseudo-fluitans* as a dominant. Certain plants are confined to certain groups of rivers, e.g. *Oenanthe fluviatilis* to the rivers in the south and *Potamogeton interruptus* to various isolated rivers, most of which seem to have a high chloride content: *Hippuris vulgaris* also is by no means ubiquitous as a river plant.

Rising from low-lying land.

The River Lark (Suffolk). Most of the rivers of East Anglia and the Fens can be included in this group. They have a pH of $7 \cdot 0$–$8 \cdot 0$ and a calcium content of about 25 parts per 100,000 $CaCO_3$. The water is usually fairly clean and the average current is slow, so that there are no torrential portions nor parts of the river bed made up of boulders. There are no sudden rises of water level, but on the other hand flood water remains in the river for some time. The vegetation is very abundant and frequently has to be cut. Mosses, except for *Fontinalis*, are absent, apart from an occasional moss on the piers and artificial embankments (see Richards (**31**)).

(a) In the fastest stretches of such rivers, where the bed consists of stones, a community with *Ranunculus fluitans* as the dominant plant is found. Its constituents are:

Ranunculus fluitans	d.	Potamogeton densus	f.
Oenanthe fluviatilis	f.	Sparganium simplex	r.
Sium erectum	r.	Fontinalis antipyretica	r.
Apium nodiflorum	r.		

Phot. 3. Silted association in River Lark. The dominant plant is *Potamogeton lucens*.

Phot. 4. Littoral association in River Lark. Summer growth of *Sparganium erectum*.

BUTCHER—STUDIES ON THE ECOLOGY OF RIVERS: I. DISTRIBU-
TION OF MACROPHYTIC VEGETATION IN THE RIVERS OF BRITAIN

Phot. 5. Littoral association in River Lark. Winter conditions to compare with Phot. 6.

Phot. 6. Littoral association in River Lark. Same place as Phot. 5.
Summer growth of *Glyceria aquatica*.

BUTCHER—STUDIES ON THE ECOLOGY OF RIVERS: I. DISTRIBU-
TION OF MACROPHYTIC VEGETATION IN THE RIVERS OF BRITAIN

(*b*) *Where the current is slow* the river bed consists of sandy gravel and *Sparganium simplex* becomes the dominant plant of the community, the composition of which is as follows:

Sparganium simplex	d.	Sagittaria sagittifolia	s.d.
Potamogeton perfoliatus	f.	Potamogeton crispus	f.
Elodea canadensis	f.	P. praelongus	r.
Callitriche stagnalis	o.	P. pusillus	r.

(see Pl. IX, phot. 2).

(*c*) *Where the current is still slower* and the river bed is composed of fine mud, vegetation is abundant and *Potamogeton lucens* becomes the dominant member of a very varied community with:

Potamogeton lucens	d.	Potamogeton pectinatus	s.d.
P. natans	f.	Sparganium simplex	a.
Nuphar luteum	f.	Potamogeton crispus	f.
Zannichellia palustris	o.	Callitriche stagnalis	o.
Sparganium erectum	r.	Scirpus lacustris	r.

(see Pl. X, phot. 3).

(*d*) Several of the rivers in East Anglia (the Gipping, Lark, Little Ouse) have been canalised, but have since fallen into neglect. As a consequence there are stretches with scarcely any current in which there is a heavy deposit of fine mud, which has become colonised by a community of plants, similar to that found on the edge of a pool or near the banks of the river. Two plants play a principal rôle in this littoral community, viz. *Sparganium erectum* or *Glyceria aquatica*, but the areas where either of these is dominant may follow each other in rapid succession. *Glyceria aquatica* appears to prefer the shallower water nearer the bank and the uppermost parts of the river. The community consists of:

(*a*) *Erect reeds:*

Sparganium erectum	d.	Glyceria aquatica	d.
Phalaris arundinacea	f.	Typha latifolia	f.
Scirpus lacustris	f.	Alisma Plantago	f.

(*b*) In open places there occur among these the common plants of the silted association mentioned above (see Pls. X and XI, phots. 4–6).

Summary of the types of rivers.

The dominant vegetation of the various types of river considered are given in Table I. This and the preceding data indicate clearly that the vegetation of a river is determined by the speed of the current, which itself determines the nature of the river bed. The destructive effects of floods are well illustrated by the general sparseness of the vegetation of rivers rising in mountainous regions (e.g. Tees and Wharfe) as compared with lowland rivers or even with those which form the outflow of a lake (e.g. River Leven, Lancashire). There is very little difference in the nature of the vegetation of the highly calcareous waters of the Itchen and the Dove, but in the latter the vegetation is sparse, whereas in the Itchen it is so plentiful that it has to be cut. This difference is probably

Table I. *Dominant plants in various types of river.*

Type of river	Range of total hardness in CaCO$_3$ parts per 100,000	Average pH	Source of river	Type of community and velocity of current in yards per hour				
				Torrential greater than 3500	Non-silted 4000 to 1500	Partly silted 1500 to 500	Silted less than 500	Littoral less than 500
Non-calcareous and acid	Less than 2·0	Less than 6·5	From the mountains	—	—	Potamogeton polygonifolius	Juncus supinus	None
			From the hills	—	Ranunculus fluitans Myriophyllum spicatum	Potamogeton nitens	Juncus supinus Callitriche intermedia	
			From the lowland bogs	None	Ranunculus fluitans Myriophyllum alterniflorum	Potamogeton polygonifolius Potamogeton alpinus	Potamogeton heterophyllus	
Slightly calcareous and almost neutral	2·0–10·0	7·0–7·5	From the mountains	Eurhynchium rusciforme Fontinalis antipyretica	Myriophyllum spicatum	Potamogeton alpinus Sparganium simplex	Callitriche stagnalis Elodea canadensis	None
Moderately calcareous and alkaline	10·0–20·0	7·0–8·0	From the mountains	Fontinalis antipyretica Eurhynchium rusciforme	Ranunculus fluitans Myriophyllum spicatum	Sparganium simplex Potamogeton perfoliatus	Potamogeton crispus Elodea canadensis	None
			From the hills	—	Ranunculus fluitans Myriophyllum spicatum	Sparganium simplex Sagittaria sagittifolia Potamogeton perfoliatus	Potamogeton pectinatus Potamogeton crispus	Sparganium erectum
Highly calcareous and alkaline	Above 20·0	7·5–8·0	From the mountains	Fontinalis antipyretica Eurhynchium rusciforme	Ranunculus fluitans Sium erectum	Potamogeton perfoliatus Sparganium simplex	Callitriche stagnalis Elodea canadensis	None
			From the hills	None	Ranunculus pseudo-fluitans Sium erectum	Sparganium simplex Hippuris vulgaris	Callitriche stagnalis Potamogeton lucens	Sparganium erectum
			From the lowland bogs	None	Ranunculus fluitans Sium erectum	Sparganium simplex Sagittaria sagittifolia	Potamogeton lucens Potamogeton pectinatus	Sparganium erectum Glyceria aquatica

due to the larger floods that occur in the Dove. The difference between calcareous, non-calcareous and acid streams seems to be one of degree and one type of river merges into the other. There are, however, as Watson (**36**) has pointed out, some plants that are only found in highly calcareous rivers and some that only occur in acid waters. On the other hand, as the vegetation lists show, a large number are to be found indifferently in all kinds of waters.

In the various rivers considered there are almost always two distinct types of vegetation, one in the fast-flowing stretches with a bed of stones, another in the slow-flowing parts with a bed of sand and mud. They are designated the *non-silted* and *silted* communities respectively. In all very fast rivers there is also a sparse community growing on rocks and boulders and designated the *torrential* community. At the other extreme, in muddy portions of slow-flowing rivers and canals, there occurs a growth of plants described as the *littoral* community because it consists of plants that usually occur on the shores of lakes and ponds. Intermediate between the silted and non-silted communities one can distinguish yet another type, designated the *partly silted* community, which comprises plants usually found on fine gravel.

The dominant plants of these different communities are given in Table I. The torrential community is dominated by mosses, the non-silted community by *Ranunculus fluitans*, *R. pseudo-fluitans* and *Myriophyllum spicatum*, the latter having a preference for non-calcareous waters. The partly silted community is more varied, but *Sparganium simplex* and certain species of *Potamogeton* are usually dominant in all waters, and in addition *P. perfoliatus* and *P. crispus* are abundant in calcareous waters. The silted community is dominated by *P. lucens*, *P. pectinatus* and *Callitriche stagnalis* in calcareous rivers, and by *Juncus supinus* and *Potamogeton heterophyllus* and various other plants in acid waters.

Effect of artificial changes on the vegetation.

The preceding observations will have shown that the most productive river and the one likely to fulfil best the functions outlined on p. 68 is one in which conditions are not extreme and in which the water is neither very deep nor turbid.

On the one hand, rise and fall of the water causing pronounced floods leads to a vegetation which is too sparse, while slow-flowing rivers, such as those of the eastern counties, often harbour too much vegetation. Deposition of silt at first increases the fertility of a river, but an excess is certainly deleterious, because as shown by Butcher, Pentelow and Woodley (**11**) the layers of water above the silt become deoxygenated and the fauna is neither so varied nor so plentiful. The "ideal" river will have alternate fast-flowing and slow-flowing stretches, little flooding, yet sufficient occasional rise of water to prevent too great an accumulation of silt.

The above-mentioned changes introduced by man, viz. canalisation, building

of dams and abstraction of water, have all tended to cause rivers to diverge from the ideal condition because they usually increase the deposition of silt. These alterations interfere most with small and slow-flowing streams; in fast-flowing rivers such changes tend to bring about less extreme conditions and in them a certain decrease of current and more deposition of silt are all to the good.

Effect of sewage pollution.

A large number of English rivers receive a greater or less amount of domestic sewage in various stages of purification. Gross pollution results in the stream becoming barren save for the various species of sewage fungi and Protozoa and a few oligochaetes and chironomids which can live in the deoxygenated water. Sewage has three main effects on a stream: (1) deoxygenation of the water, (2) silting, (3) introduction of organic matter and therefore increase of fertility. Deoxygenation does not at first affect the macrophytic flora, but later there is a distinct weakening of the stock. There is always a large quantity of fine silt in a sewage effluent and more is frequently precipitated from the colloidal organic suspension as the effluent mixes with the river. The growths of the sewage fungus community collect this fine silt which in a fast river would not otherwise be deposited. Thus the river bed becomes covered with organic silt, so that the vegetation will belong to the silted community even in a river which is fast flowing. This is well exemplified by Fig. 3, which is a plan of the River Lark at Lackford. Sewage enters the river at *AB*, and along its track one finds a characteristic silt-loving plant, *Potamogeton pectinatus*, whereas the rest of the vegetation is that typical of the non-silted community.

The effect of the large quantity of sewage brought into the Tees by the River Skerne is seen in the increased quantity of macrophytic vegetation and particularly in the growth of masses of *Cladophora glomerata* in the months of May and June. The extent of this growth can be seen in Pl. XII, phots. 7 and 8. As this alga grows best in the gravelly and free-flowing stretches of the Tees several miles below its junction with the Skerne, there seems no doubt that it is the food material present in the sewage and not the silt that causes this huge growth. There is, however, the possibility that the increase in the calcium content of the Tees due to the Skerne is responsible. The distribution of *Cladophora* in the river elsewhere is against this assumption, and the figures given in Table II suggest that organic matter is the determining factor. This alga grows in abundance in the River Balder at Balder-Foot, though not in the River Lune. Both these are streams of soft water and tributaries of the Tees, and the only difference between them is that the former receives sewage and the latter does not. The conditions are best seen in Table II.

From this table it is clearly indicated that *Cladophora* grows where organic matter is high as shown by the abundance of nitrogenous matter and absorbed oxygen.

Phot. 7. River Tees at Eryholme in June 1929 showing growth of *Cladophora*.
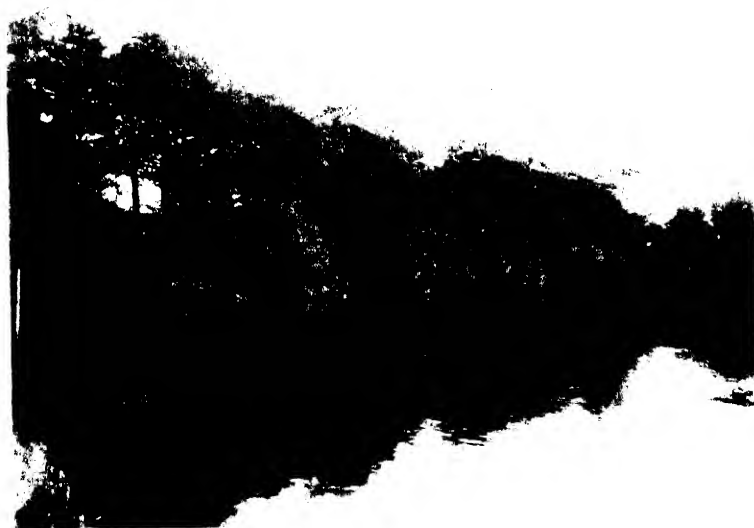
Phot. 8. River Tees at Eryholme in July 1929 after a flood had washed away the growth of *Cladophora*.

BUTCHER   STUDIES ON THE ECOLOGY OF RIVERS: I. DISTRIBUTION OF MACROPHYTIC VEGETATION IN THE RIVERS OF BRITAIN

Table II.

Expressed as parts per 100,000

Position	Hardness in terms of CaCO₃	Free ammonia as N₂	Albu-minoid ammonia as N₂	Organic N₂	Oxygen absorbed in 4 hours at 80° F.	Remarks
Eryholme (River Tees)	10	0·028	0·034	0·114	0·959	*Cladophora* very abundant
Below Barnard Castle sewage works (River Tees)	8	0·018	0·018	0 054	0·603	*Cladophora* plentiful
Above Barnard Castle (River Tees)	8·5	0·012	0·03	0·212	0·231	*Cladophora* absent
High Force (River Tees)	6·5	0·012	0·025	0·06	0·758	*Cladophora* absent
Balder-Foot, Cotherstone (River Balder)	5·75	0·032	0·038	0·08	0·989	*Cladophora* abundant
Mickleton (River Lune)	6·0	0·0005	—	—	—	*Cladophora* absent

There are no flowering plants in the Tees above its junction with the Skerne, but there are a number below that point in spite of the faster flow. The dominant plant is *Potamogeton interruptus*, a species that usually occurs in the partly silted association on gravel and is not found on stones. It is not clear at present whether this change is due to the silt from the sewage or its chemical composition (though probably the latter) because the food supply of rooted plants is dependent on the river bed and what is there deposited.

There is every indication from other observations that an increased volume of vegetation and the replacement of the non-silted by the silted community are a general effect of sewage pollution in all rivers.

V. Biological problems.

The growth and mode of spread of the macrophytic vegetation of streams has been studied by means of quadrats in the River Itchen and the River Lark, and some of them are reproduced in Figs. 2 and 3. The Itchen at Alresford is a narrow stream 4½ metres wide with a current flowing at the rate of about one mile per hour. The transect selected was 10 metres long and extended across the entire width of the stream. In the lower half of the transect the plants were dug out of the river bed in order to create a bare patch where colonisation could be studied. The vegetation on the transect was plotted four times a year for three years.

The River Lark at Lackford in Suffolk has a considerably slower flow than the Itchen, but the place chosen for the transect was one of the swiftest in the river (current about 0·5 miles per hour). This spot was selected because the sewage effluent that enters at *AB* (Fig. 3) brings considerable quantities of silt, and the changes due to its deposition are well shown. This transect was 6 by 10 metres and the vegetation was plotted three times in the course of two
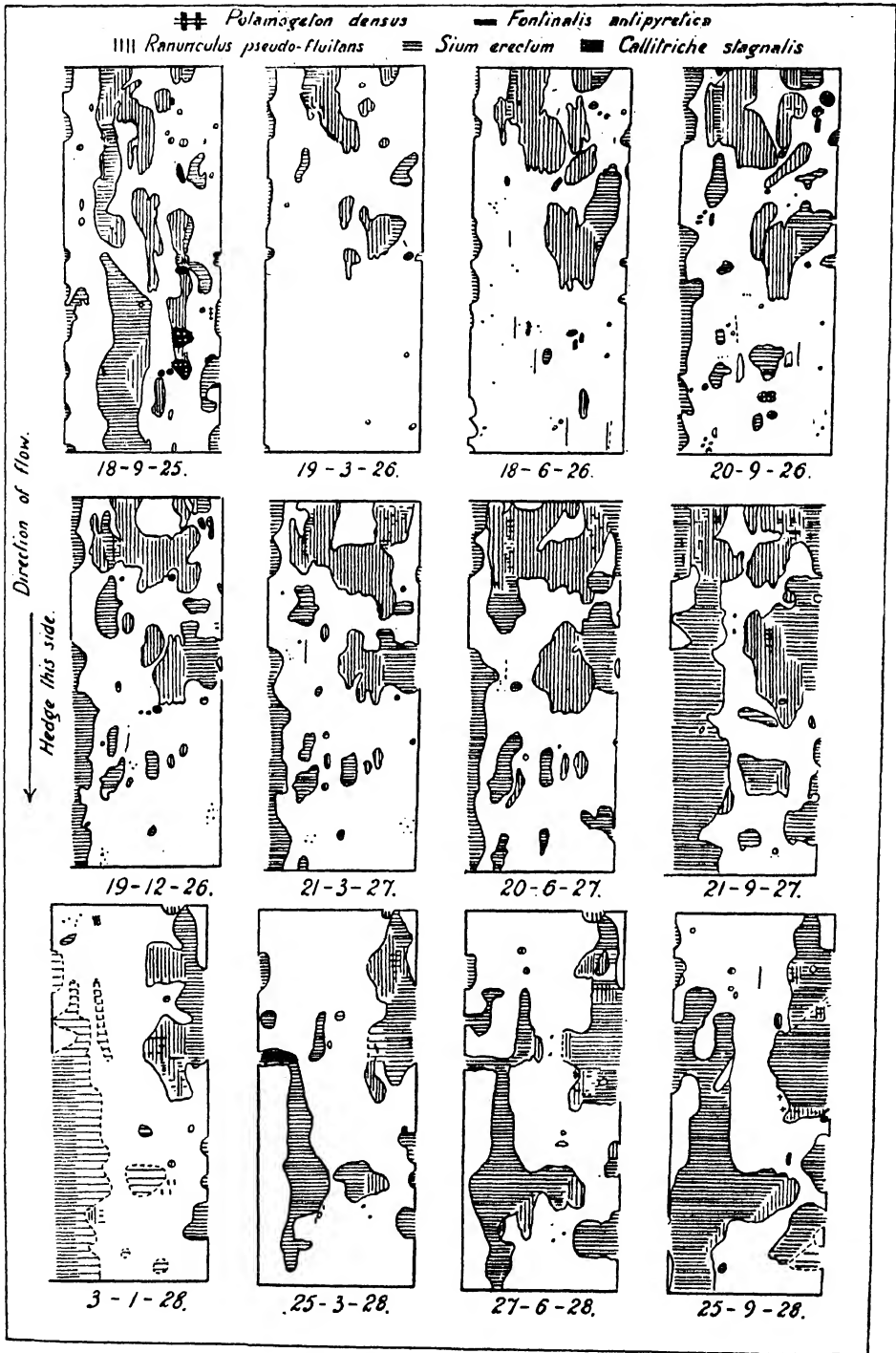
FIG. 2. Diagrams of plants in River Itchen transects. (Scale 1 cm. = 1 m.)
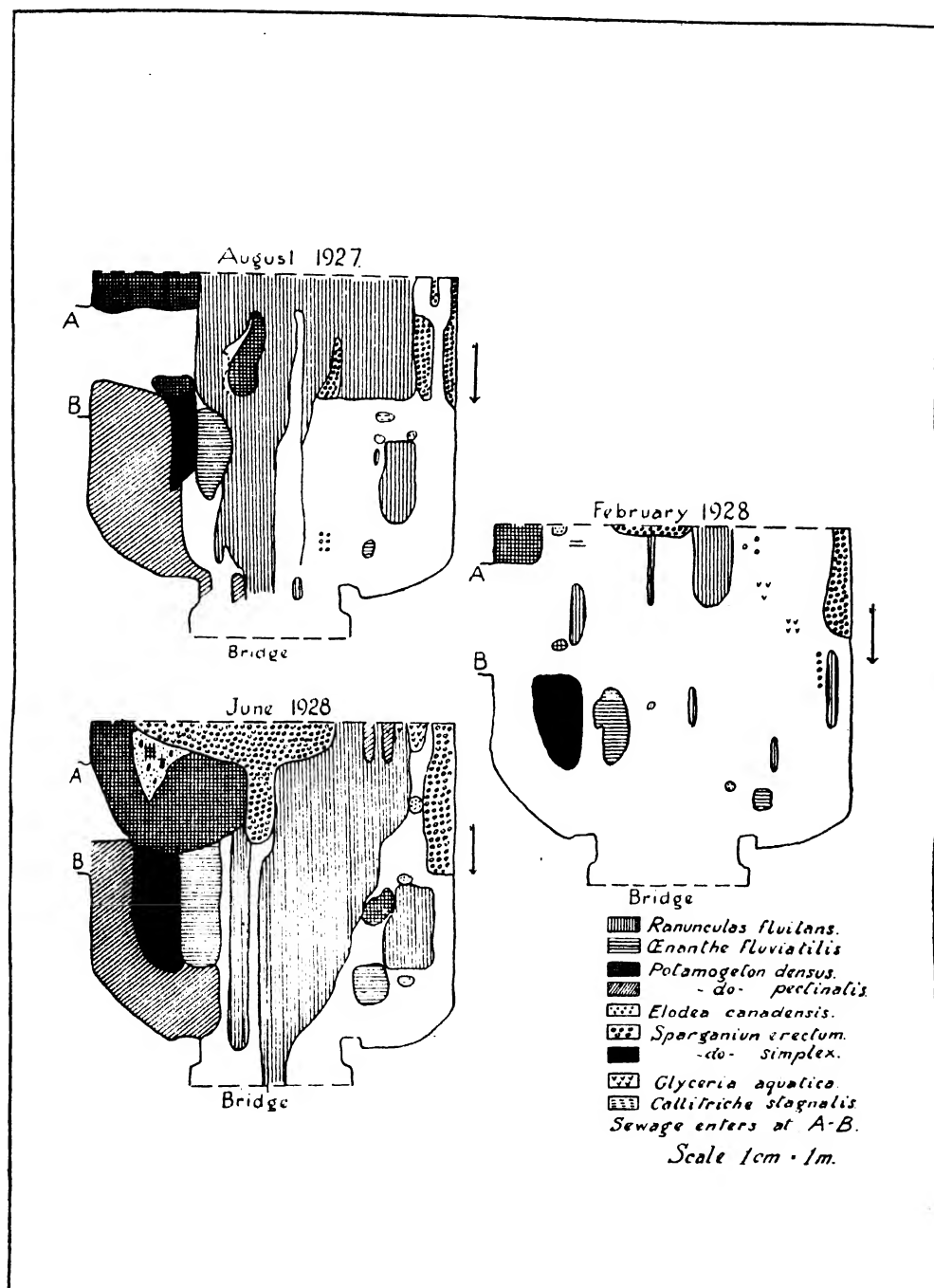
FIG. 3. Diagram of vegetation in the River Lark transect.

years. The plants found on the respective plots in the two rivers were as follows:

River Itchen.

Ranunculus pseudo-fluitans
Sium erectum
Callitriche stagnalis

Potamogeton densus (only in the dug up plot—
    never reappearing)
Fontinalis antipyretica
Vaucheria sp.

River Lark.

Ranunculus fluitans
Potamogeton pectinatus
P. densus
Sparganium erectum
S. simplex

Sium erectum
Callitriche stagnalis
Oenanthe fluviatilis
Elodea canadensis

The results obtained from the study of these transects clearly demonstrate some of the most important biological problems of river vegetation to be considered below.

A. *Impermanence of vegetation.*

In the first place it is evident that the vegetation is not permanent. No two charts of the same plot are alike. The plants tend to move downstream into unoccupied areas, while those areas recently occupied are left bare. This is well shown by the strip of *Sium erectum* on the left-hand side of the Itchen transect. It originated from the growth along the bank and spread towards the centre. The flood of December, 1927, thinned out the portion in the open water away from the bank, but did not affect the thick growth in the more protected portion. Yet in the following March the region near the bank was quite bare, whilst there was a dense growth in the open water. This is just the reverse of what would happen on a piece of waste land, if the plants on a part of it were thinned out. It raises the question whether the places in which the *Sium erectum* disappears have become sterile. This is a possible explanation because, as emphasised above, such submerged plants obtain their food from the river bed and not from the surrounding water. The river bed is moreover stony owing to the strong current and there is no appreciable deposition of silt, so that some time will elapse before the fertility of such an area is restored. The stronger the current, the more marked one might expect this effect to be. This factor, together with the destructive action of the floods already considered (p. 64), accounts for the poverty of vegetation in streams with pronounced flood and strong currents which involve a stony bed and little deposition of silt.

B. *Seasonal growth.*

One of the most striking differences between the Lark and Itchen transects lies in the seasonal variations of growth. Table III and Fig. 4, which give the areas occupied by the two dominant plants in the Itchen transects, show that there was a continual increase of *Sium erectum* throughout the three years, an

increase which was momentarily checked only by the floods of December 26th–31st, 1927.

Table III. *Area occupied by* Sium erectum *and* Ranunculus pseudo-fluitans *respectively in the transect of the Itchen at Alresford.*

	Upper half		Lower half		
Date	Area occupied by *Sium*	Area occupied by *Ranunculus*	Area occupied by *Sium*	Area occupied by *Ranunculus*	Remarks
	sq.m.	sq. m.	sq.m.	sq.m.	
Sept. 1925	1·03	2·79	7·07	1·48	Before digging up
March, 1926	1·92	2·88	0·04	0·08	
June, 1926	2·51	4·52	0·54	0·66	
Sept. 1926	2·21	4·72	2·50	1·02	
Dec. 1926	3·33	4·02	3·20	0·62	
March, 1927	2·07	4·23	2·60	0·18	
June, 1927	3·29	8·06	4·05	1·09	
Sept. 1927	7·79	4·87	8·40	1·15	Floods came December 26th–31st
Jan. 1928	3·57	0·93	5·52	0·08	
March, 1928	4·15	0·91	3·32	0·27	
June, 1928	7·00	0·97	5·10	0·83	
Sept. 1928	8·24	0·43	9·67	0·64	

Total area 20 sq.m.   Total area 20 sq.m.

See also Fig. 4.
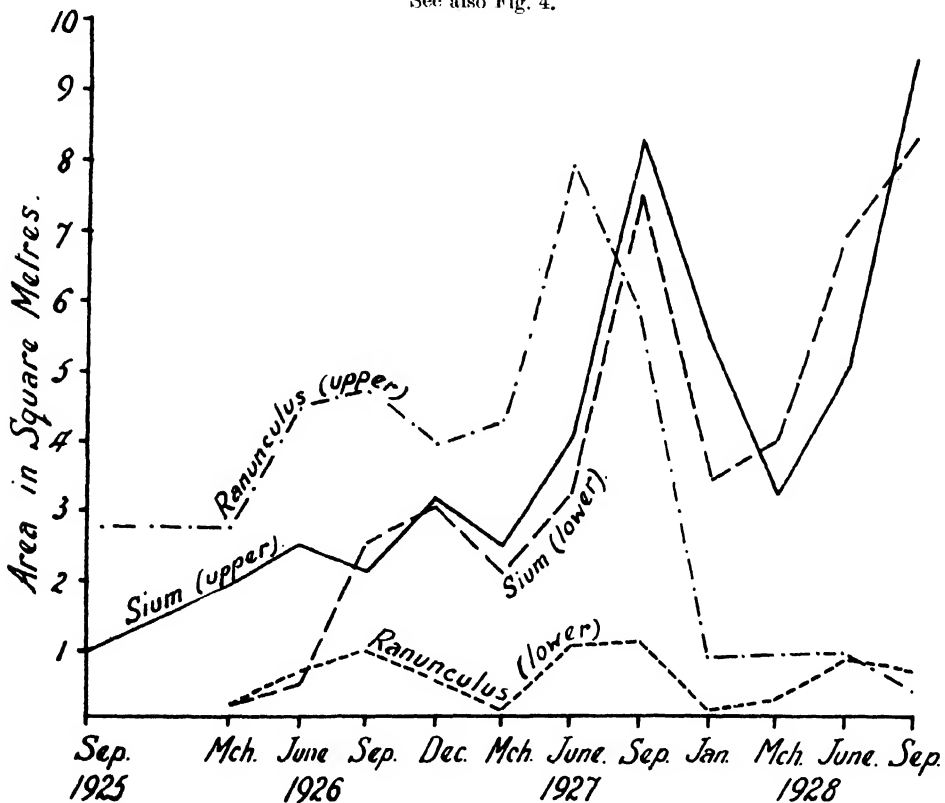
FIG. 4. Area occupied by dominant plants (*Sium erectum* and *Ranunculus pseudo-fluitans*) in two transects (upper and lower) of River Itchen.

In the case of the River Lark there is no such continuous increase, since most of the plants die away in the autumn and grow rapidly again in the spring. The same sequence of events as in the Itchen is to be observed in the Tees, where *Ranunculus fluitans* and *Potamogeton interruptus* persist throughout the year, whereas the changes in the Lark are similar to those in an ordinary pond.

Sufficient data have not yet been collected to account fully for this dying down of the vegetation in some cases and not in others, but possible causes that may be considered are (*a*) that the habit is inherent in certain species, (*b*) that the habit is due to environmental conditions, and (*c*) that it is a temperature effect.

(*a*) *The tendency to persist* or to die down in winter appears to be inherent in many species of aquatics, as shown by the persistence of *Callitriche*, *Elodea*, *Potamogeton densus* and *Oenanthe fluviatilis* both in the Lark and the Itchen, while the Potamogetons that occur in the silted associations of the Lark die down: there are, however, no members of the silted association present in the plot on the Itchen to compare with the Potamogetons in the Lark. The following are tentative lists of species that do and do not die down in winter:

(1) *Species that do not die down.*

Apium nodiflorum	Potamogeton densus
Callitriche stagnalis	P. interruptus
Elodea canadensis	Ranunculus pseudo-fluitans
Hippuris vulgaris	R. fluitans
Myriophyllum spp.	R. sphaerospermus
Nasturtium officinale	Sium erectum
Oenanthe fluviatilis	

(2) *Species that die down.*

Alisma Plantago	P. crispus
Nuphar lutea	P. lucens
Polygonum amphibium	Sparganium erectum
Potamogeton natans	S. simplex
P. perfoliatus	Sagittaria sagittifolia

(*b*) *The nature of the habitat* may bear some relation to this phenomenon, since wholesale dying down is least marked in quickly flowing waters. Such an interpretation is also suggested by the fact that *Callitriche stagnalis* is greatly reduced in quantity in the winter in ponds, but not markedly so in a flowing river. The difference may be due to the rigorous habitat afforded by a fast-flowing stream, where the difficulties of maintaining a hold and of increasing in area are great, so that the summer increment is small. The loss due to continual washing away is great compared to loss due to death in autumn, so that there is little marked change between winter and summer. In a slow-flowing river on the other hand the environment permits of a great summer increase, loss due to washing away is small compared to loss due to death in the autumn, and the comparatively small amount of vegetation which persists through the winter (though actually almost as great as the average in a fast river) is very inconspicuous.

Also the cause may lie partly in the partial sterilisation of the bed of the river, since, to render this fertile, silt and organic débris must again be deposited. In a slow-flowing stream or pond, deposition is almost continuous, and is greatest after the death of the aquatic plants in the autumn. In swift rivers a much longer time will be required to render the sterile portions fertile, because silt and organic materials are not deposited but only trapped in small quantities among the stones and patches of plants. Further, there is no sudden release of organic matter by wholesale death of the plants.

(c) *Temperature* does not appear to exercise much effect. The temperatures of both rivers taken within 10 yards of the transect are given in Table IV, and there is evidently no relation to the survival of the plants, whether one compares temperatures for successive years in the Itchen, or for the Itchen and the Lark in the same year. Thus the higher temperatures of the Lark in winter do not lead to the survival of the plants under discussion.

Table IV. *Mean monthly temperatures (° C.) in rivers Itchen and Lark.*

	River Itchen (at Alresford)			River Lark (at Icklingham)	
	1926	1927	1928	1927	1928
Jan.	—	5·3	6·1	6·8	4·9
Feb.	—	5·5	6·6	8·2	8·2
March	—	7·3	7·3	8·4	8·6
April	9·2	8·6	—	9·1	—
May	10·8	11·1	—	12·9	—
June	12·4	11·8	—	13·9	—
July	14·1	12·9	—	16·9	—
August	13·5	12·7	—	15·8	—
Sept.	12·0	10·7	—	14·2	—
Oct.	7·8	9·2	—	10·2	—
Nov.	6·9	7·0	—	7·8	—
Dec.	5·4	5·2	—	6·4	—

C. Colonisation.

The colonisation of an area by new plants is shown in the lower portion of the Itchen transect. It is possible that the lower plot was not completely denuded of all its plants, since some occupy positions at the end of the three years similar to those which they occupied at the beginning. There are, however, pronounced differences. Thus *Potamogeton densus* did not reappear on the plot during the three years. *Sium erectum* colonised all the left-hand portion of the plot by extension, at various seasons, from the untouched upper portion. This plant spread at a great rate on to the bare areas and such growth was far more extensive than that due to any persisting fragments, whether accidentally left when denuding the plot or representing portions perennating from season to season. The area occupied by *Ranunculus* is too small to admit of any generalisations; there are numerous small patches of this plant which have changed their position so frequently that as much can be found in new as in old areas.

On the whole the plot indicates that the new colonies were derived from portions of the plants in the river bed above, since the new plants are in direct

line with the colonies of the same plants in the plot above. Colonisation is fairly rapid, for within one year the plants occupied half the original area covered and in two years as much space as was originally covered.

D. *Effect of macrophytic vegetation on current and depth.*

The effect of an extensive growth of rooted vegetation on depth and current is well shown in the River Lark (Fig. 5). The dense growth of plants in this river arrests the flow of the water to a marked extent and holds it back. Records of water-level at Lackford bridge show that the level of the river rose
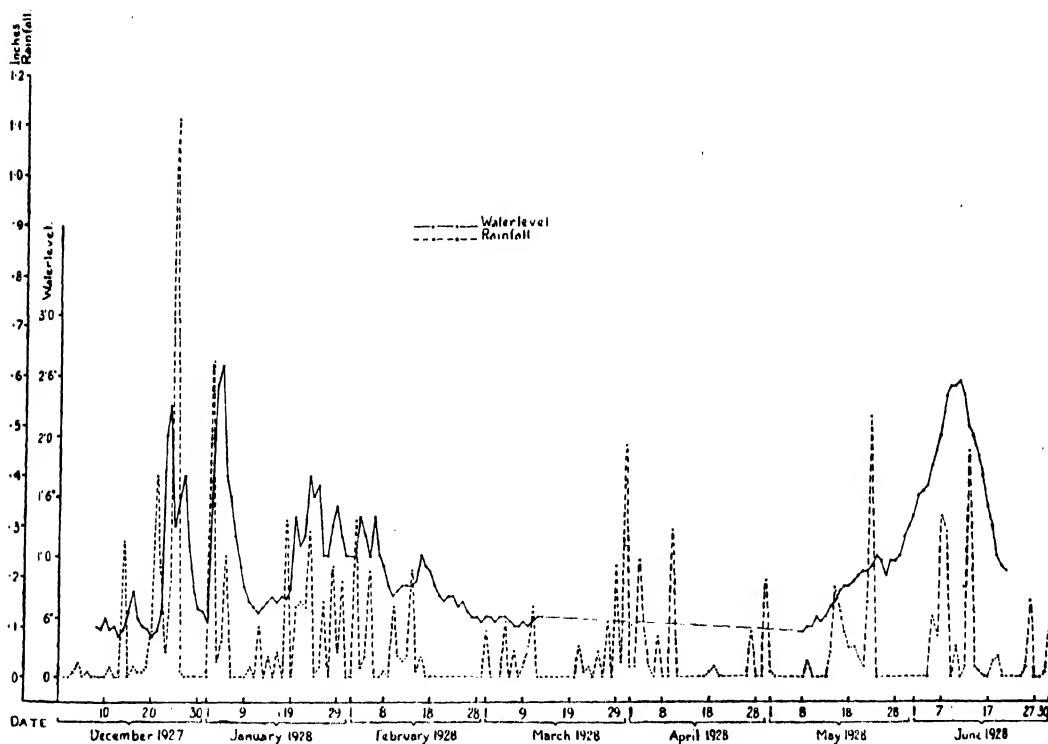
Fig. 5. Diagram of water-level and rainfall at Lackford Bridge.
(Reproduced from Butcher, Pentelow and Woodley (11).)

gradually but continually during May, when the macrophytic vegetation consisting of *Potamogeton lucens, P. pectinatus, Sparganium erectum* and *S. simplex* was growing rapidly, and fell again when the vegetation from Lackford to Icklingham (a distance of two miles downstream) was cut by the miller in order to augment the water supply for his mill at Icklingham. There was little rain during this period, and since the mill referred to is two miles downstream, no altering of sluices could have produced so marked an effect (see Fig. 5). While the vegetation was so dense the river was frequently 24 in. below the normal level at this mill and 20 in. above normal at Lackford. It is obvious that as the water does not get away the current must be reduced

by so dense a growth of aquatics, and this reduction leads to a greater deposition of silt on the river bed, so that at length such reaches have to be thoroughly cleaned out if the river is to fulfil its proper functions.

E. *Macrophytic vegetation as a habitat for plants and animals.*

The importance of macrophytic vegetation as a shelter for animals is emphasised by Percival and Whitehead (26) as well as by Butcher, Pentelow and Woodley (11). It was shown by these workers (1) that the community of animals in the weeds is the same as that normally inhabiting a stony river bed; (2) that the numbers of animals found on the various species of plants were not markedly different, save that fewer were found on the leaves of *Sparganium simplex*. This is probably due to the fact that the thin undivided leaves afford neither the surface nor the shelter that is provided by those of such plants as *Ranunculus fluitans* or *Fontinalis*. The water plants are also of importance to that group of fishes (the Cyprinodea) who lay their eggs among these weeds. Many of the sessile algae that grow on the bed of a stream, whenever the light intensity is sufficiently great, also grow on the stems and leaves of the aquatics. As a consequence the larger the area of rooted vegetation the greater the number of epiphytic algae that can establish themselves. Since such algae, especially the diatoms, are the chief food of the smaller animals (see Percival and Whitehead (27)) the rooted vegetation plays an important rôle also in this respect.

F. *Relation of macrophytic vegetation to the fertility of a river.*

There are two ways in which the macrophytic vegetation increases the fertility of a river. First, there is the holding up and trapping of silt, including the finer organic muds, which are usually rich in nutrient substances and which, if there were no effective barrier, would be carried out to sea. This trapping of silt and nutrient materials takes place even in fast rivers, as is well illustrated in the River Tees at Low Middleton (see p. 64). Secondly, as pointed out by Pond (29), since these plants obtain their mineral salts from the substratum their death and decay result in the enrichment of the water with mineral matter which becomes available for the growth of the algae.

Kofoid (19) showed that in pools containing only non-rooted macrophytes (*Ceratophyllum*) there was very little plankton. A rather different state of affairs obtains in a river. In the first place most of the algae grow on the river bed and are presumably as dependent on the nutrient matter passing into solution from the silt, as on that brought down by the river from above. In the second place the remains of the plants which have died away are washed downstream and take the nutrient material with them. In this respect, however, it is necessary to distinguish two different types. In slow-flowing rivers (e.g. the Lark), where there is wholesale dying down of the vegetation in autumn, there is a sudden increase of dead and decaying organic material which, owing to the

slight current, is not carried far downstream. In fast-flowing rivers (e.g. the Itchen), where much of the vegetation persists, the liberation of organic materials is much more gradual. The presence of this larger quantity of organic material—well shown in the River Lark (*loc. cit.*)—is obviously one reason why a slow-flowing river tends to be more fertile, to have a more abundant flora and to exhibit more extensive variations than a fast stream.

Not only do the plants trap passing silt and nutrient materials, but their rhizomes and roots must play the same rôle as those of sandhill plants in consolidating the substratum in which they live. A sandy river bed covered with vegetation is not liable to undergo much shifting. It can also be demonstrated that littoral vegetation protects river banks in times of floods, e.g. those of the Lark at Hengrave. By careful cultivation of submerged plants open channels can be maintained in the middle of the stream which will take most of the water, leaving the weedy portions near the banks well protected and inhabited by an abundant fauna and this will be the feeding ground of fish. Percival and Whitehead (27) point out that at certain places in the River Wharfe the stones are being continually rolled over by the current so that the fauna among them is very poor. But occasional stones in the same locality which are overgrown with *Fontinalis, Eurhynchium* and even *Lemanea* shelter an abundant fauna. The rooted plants will help materially to cement the loose stones to the river bed by growing all round and over them, and in this way also they tend to increase the general fertility of the fast stretches.

G. *Importance of macrophytic vegetation.*

From the above considerations it may be seen that the macrophytic vegetation is probably of fundamental importance in the general biological character of a river. This is in marked contrast to a deep lake where rooted vegetation is scarce compared with the volume of water, and the phytoplankton represents the biological community that has most influence on the conditions of the lake generally and especially on the fauna. It is a well-known fact that in the small calcareous streams of Southern England, and particularly in those that are slow flowing, the vegetation can be so plentiful as to require continual cutting, whereas the phytoplankton (potamoplankton) is small in amount, unimportant, and recruited chiefly from the algae found on the river bed and on the larger aquatics. Where vegetation is dense it can play an important part in determining the physical characters of a river by holding up the water, hindering the flow, producing local eddies, cementing the river bed and trapping, or causing to be deposited, silt and nutrient materials. It is also a source of fertility to the river, taking mineral salts from the substratum and, on death, liberating a considerable amount of organic and mineral matter to those portions of the stream where it is trapped or deposited. It is also an important agent for the oxygenation of the water, though, unlike the microflora, it does not supersaturate the water to any extent.

Though in itself not a source of food for the great majority of animals inhabiting a river, it has a great influence on their quantity and distribution by acting (1) as an area for the growth of epiphytic algae which are the chief source of food of the smaller fauna, (2) as a source of oxygen, (3) as a shelter and habitation, and (4) as an agent for cementing stones and gravel where much of the fauna is found.

In a fast-flowing river macrophytes are not so plentiful, yet it is here that their presence is most valuable, especially because they act, as shown above, as a shelter and an agent for stabilising the river bed.

SUMMARY.

The chief factor which governs the distribution of the larger plants or macrophytes in running water is current. As well as exerting a mechanical strain on the plants, current determines the nature of the river bed, which, in its turn, determines the type of vegetation. Torrential, non-silted, partly silted and littoral communities of plants are distinguished and shown to be correlated with the nature of the river bed which consists of rock and boulders, stones, gravel, silt or mud respectively in the above communities.

The quantity of the vegetation is continuously reduced in rivers with large and sudden floods. The nature of the communities is modified by the calcium content of the water, by excessive silting and by pollution.

By quadrat studies it is demonstrated (1) that some plants persist throughout the year while others decay in the autumn and (2) that vegetation is impermanent and tends to move to unoccupied portions of the river bed leaving the other parts barren. Macrophytic vegetation can modify the physical conditions in a river by consolidating the bed or collecting silt and, in some streams, can grow to such an extent that it holds up the water and causes floods. Macrophytic vegetation acts as a habitat for animals and algae and largely determines the fertility of a river.

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THE VEGETATION OF ST KILDA

By C. P. PETCH.

(With one Map in the Text.)

INTRODUCTION.

IN the summer of 1931 the now uninhabited island of St Kilda, most westerly of the Outer Hebrides, was visited by a party of six from the Universities of Oxford and Cambridge. This island has recently attracted considerable attention by reason of the evacuation of the inhabitants, remnants of a population that had lived there from the earliest recorded times. On their departure they took with them some 1300 sheep. After being under the hand of man for many centuries the island thus lapses into an almost natural state. The scientific significance of this is at once apparent. Owing to the removal of the biotic factors of grazing and cultivation, the future development of the vegetation may be regarded as a large-scale experiment in plant ecology. A survey of the present conditions was therefore undertaken, which revealed several interesting features, particularly the influence of the numbers of sea birds which have their nests there.

Lying 50 miles west of Harris, and about 150 miles from the mainland of Scotland, the St Kilda group, as it is more correctly described, contains four islands and a number of small rocks and stacs. Only the largest island, Hirta, was permanently inhabited. This is 1515 acres (637 hectares) in extent, its greatest length and breadth being 2½ by 1¾ miles (4 × 2·8 km.). Except for the beach in Village Bay on the south-east side Hirta is completely surrounded by cliffs, which rise on the north coast to 1300 ft., forming the highest cliffs in the British Isles. Topographically Hirta consists of two valleys, facing north-west and south-east, surrounded by five peaks, Conachair (1397 ft.), Mullach Mòr (1172 ft.), Oiseval (948 ft.), Mullach Bi (1164 ft.), and Mullach Sgar (715 ft.).

The vegetation may best be considered under three headings:

I. The moorland, covering most of the area.

II. The abandoned arable land.

III. Maritime communities, including those of the lower cliffs and of moorland areas within reach of sea spray.

No trees, or shrubs larger than heather are found on the island.

I. THE MOORLAND.

This is the most typical and widespread plant community. It is dominated by heath grasses (*Festuca ovina, Nardus stricta*) and gives a green appearance to the hills when seen from the sea, which is strikingly different from the purple heather moorlands of the Dee and Tay valleys. *Calluna vulgaris* is everywhere

present, but does not grow above the level of the turf, which is close and thick as though heavily grazed. Well-grown bushes of heather are only found in

ST KILDA

Gob na h'Airde

The Cambir

Glen Bay

△1396·8
Conachair

Mullach Mòr
1172

Gleann Mòr

Mullach Bì
1164

Lover's Stone

926

Mullach Sgar △ 715

Oiseval
948△

Village Bay

Rudha an Uisga

Ruaival

DÙN

0   ¼   ½   ¾   1 mile

Scale: two inches to one mile.

Heights in feet

Arable and semi-arable

Puffin areas

Moorland affected by sea spray

Cotton-grass bogs

Sheep enclosures

Unmarked areas represent moorland

Curved lines denote cliff

MAP 1.

cracks of the vertical rock faces which must have been inaccessible to sheep. The abundance of *Calluna* is thus not evident until the turf is examined close at hand. *Erica cinerea* and *Vaccinium myrtillus* are found in the same condition though more rarely. Now that all grazing has been stopped it seems

probable that an increase of *Calluna* and other heath shrubs will occur at the expense of the grasses. In order to have some measure of the degree to which this has proceeded at the time of any subsequent visit to the island two permanent quadrats were established, one on the slopes of Oiseval, the other on flatter land near the village. *Calluna* prefers the shallower and drier soil patches, and avoids bogs and regions exposed to sea spray.

The vegetation of this community is very varied so that it merges into that of the bogs and of the cliffs. Owing to the difficulty of estimating the composition of the turf over such a large area, thirty sample square metre plots were marked out at random, and the frequency of the plants included noted. The samples ranged from 200 to 1100 ft. above sea-level and had an average altitude of 500 ft. The results were as follows[1]:

	Frequency	Average abundance		Frequency	Average abundance
Antennaria dioica	1	f.	Leontodon autumnale	3	o.
Anagallis tenella	2	o.	Luzula campestris (agg.)	2	r.
Anthoxanthum odoratum	4	f.	L. sylvatica	1	r.
Agrostis canina	3	f.	Molinia caerulea	2	o.
A. palustris (agg.)	4	f.	Nardus stricta	5	f.
Aira praecox	1	o.	Narthecium ossifragum	1	o.
A. flexuosa	1	o.	Orchis maculata	2	r.
Blechnum spicant	1	r.	Polygala vulgaris	3	o.
Calluna vulgaris	4	o.	Potentilla erecta	5	f.
Carex binervis	2	o.	Pedicularis sylvatica	3	r.
C. flacca	1	?	Prunella vulgaris	1	o.
C. flava	2	o.	Pinguicula vulgaris	2	o.r.
C. panicea	4	f.	Plantago lanceolata	3	o.
C. pilulifera	4	o.	P. maritima	4	f.
C. pulicaris	3	o.	P. coronopus	1	r.
C. rigida	1	r.	Rhinanthus drummond-hayi	1	r.o.
Cerastium vulgatum	1	r.	*Ranunculus acris	1	r.
Empetrum nigrum	1	a.	*R. flammula	1	o.
Erica tetralix	1	a.	*Rumex acetosa	1	r.
E. cinerea	1	a.	Salix repens	1	f.
Euphrasia vulgaris	5	o.	Scabiosa succisa	2	o.
*Eriophorum angustifolium	1	f.a.	Scirpus caespitosus	2	o.
Festuca ovina (agg.)	5	f.	Selaginella selaginoides	3	o.
Galium saxatile	3	o.	Sieglingia decumbens	5	o.
Gentiana campestris	1	r.	Thymus chamaedrys	3	f.
Hypericum pulchrum	2	r.o.	Trifolium repens	1	f.
*Holcus lanatus	1	r.	Vaccinium myrtillus	1	a.
*Hydrocotyle vulgaris	1	r.	Viola riviniana	5	o.
Juncus lamprocarpus	1	r.	V. palustris	1	r.o.
J. squarrosus	1	o.			

To these must be added certain local species which were too rare to be included in any samples:

Botrychium lunaria   Schoenus nigricans
Hymenophyllum unilaterale   Silene acaulis
Lycopodium selago   Veronica officinalis
Malaxis paludosa   Vaccinium vitis-idaea
Sagina procumbens

[1] The names used throughout are those of the *London Catalogue of British Plants*, 11th ed., 1925. The frequency data are comparable to those obtained by **Tansley** and **Adamson** (4), but the percentage figures have been referred to five classes: the average abundance figures have been obtained in the same way as in their next paper (5), but here the numerical averages have been translated back to letters.

Species in the list marked with an asterisk are not considered true members of this community. Several new records for the island are included, but these are considered in another paper (6).

The altitudinal distribution of these plants presents no striking features. *Vaccinium myrtillus*, *Lycopodium selago*, *Luzula sylvatica* and *Carex rigida* do not descend below 600 ft., *Empetrum nigrum* not below 700 ft., and *Vaccinium vitis-idaea* not below 1000 ft. On comparing ten lowland quadrats (100–400 ft.) with ten upland ones (700–1100 ft.) a lowland tendency was noticeable in *Anagallis tenella*, *Scabiosa succisa*, *Juncus lamprocarpus*, *Plantago lanceolata*, *P. maritima*, *Pinguicula vulgaris*, *Carex panicea* and *Molinia caerulea*, and an upland preference in *Galium saxatile*, *Pedicularis sylvatica*, *Polygala vulgaris*, and *Carex binervis*, apart from the strictly limited species noted above. Other species were more or less evenly distributed, or too infrequent in these samples to allow valid conclusions to be drawn.

Though the St Kildans were not in the habit of cutting true peats as the people of the outer Hebrides do, they removed the moorland turf in slabs a few inches deep for fuel, to the detriment of their pastures. Where this has been done, the soil washes away, leaving a stony area inhabited between the rocks by stragglers from the moorland flora. *Carex flava*, *C. goodenowii*, *C. stellulata*, *C. panicea*, *Juncus lamprocarpus*, *J. bulbosus*, *Ranunculus flammula* and *Plantago maritima* occupied such an area in the bottom of Gleann Mòr, the north-facing valley; *Carex flava*, *C. goodenowii*, *Festuca ovina*, *Agrostis tenuis*, *A. canina*, *Leontodon autumnale*, *Plantago maritima* and *P. coronopus* a similar area on the top of Mullach Sgar. The moorland is dotted with small turf and stone huts or "cleits" in which the St Kildans stored their turf fuel and other produce. Close to the walls of these, certain plants which are most abundant in the arable land are almost always to be found, viz. *Holcus mollis*, *Rumex acetosa*, *R. acetosella*, *Cerastium vulgatum*, *Trifolium repens* and *Ranunculus acris*. Their presence may be due to human traffic, disturbance of the ground in building, increased shelter, manuring consequent upon sheep seeking shelter here, or a combination of these factors. *Aira praecox* is a constant inhabitant of the turf roofs of these buildings.

(a) Bog vegetation.

On the small hills and wet stony places on the hillsides the vegetation takes on a slightly different aspect. *Ranunculus flammula* and *Eriophorum* became more abundant and such plants as *Juncus bulbosus*, *Carex stellulata*, *Potamogeton polygonifolius*, *Scirpus pauciflorus* and *Drosera rotundifolia* are found. The last two are very local in their distribution, *Scirpus* being found in one bog and *Drosera* in three.

In the flat upland regions such as the top of Mullach Mòr and on the west side of Gleann Mòr, cotton-grass bog is developed. The vegetation here is dominated by *Eriophorum angustifolium* with considerable local abundance of

Carex stellulata, Empetrum nigrum and *Scirpus caespitosus.* In addition, the moorland species occur more or less frequently, but *Calluna* and *Erica* are rare. True peat is almost always present under this community. On the top of Mullach Mòr some peat has been destroyed and erosion has taken place, leaving a peat cliff of about a foot high. It is evident that good burning peats might have been obtained from here, or from any other area covered with *Eriophorum*, but as this source of fuel was said to have been entirely neglected ((**2**), pp. 78–9), its removal in this case must be attributed to natural agencies.

(b) *Flora of high cliffs.*

By this is understood the flora of cliffs quite out of reach of the sea. This, as in the bogs, is mostly made up of plants common on the moorland, but certain species are confined to the habitat. They are:

Sedum roseum	a.	Silene maritima	o.
Angelica sylvestris	f.	Primula vulgaris	o.
Polypodium vulgare	f.	Lonicera periclymenium	r.
Salix herbacea	v.r.	Taraxacum palustre	r.
Athyrium filix-foemina	f.	Rumex acetosa	f.
Lastrea dilatata	f.		

Rumex acetosa and *Angelica sylvestris* are also found on the arable land. *Plantago maritima* is very abundant in rock cracks.

In spite of the fact that the cliffs of St Kilda are the highest and most extensive in the British Islands, nothing in the nature of a definite rock community can be distinguished, and apart from the intrusion of the eleven species noted above, the vegetation resembles isolated patches of moorland growing in such cracks and ledges as afford a foothold. This may be related to the granitic nature of the rock, which, in the Scotch mountains, is associated with a poor flora (**3**). The screes below the inland cliffs show no peculiarities except that they form the habitat of *Asplenium adiantum-nigrum*, which is only found among the boulders on the south side of Conachair. Other ferns from the cliffs have established themselves here, but the screes of smaller rock fragments are barren. *Saxifraga oppositifolia* is confined to one locality on the south side of Conachair, on wet rocks in the neighbourhood of the Amhuinn Mhòr, a rather specialised habitat which appears to resemble the high cliffs more than anything else.

(c) *Puffin colonies.*

The lower regions of the cliffs which surround the island are the home of vast colonies of puffins. Usually the cliffs are too steep to support much vegetation, but in some places, particularly on the island of Dùn, the puffin burrows occur in or above land sufficiently flat to support a grass community. Though the conditions are such as would normally lead to the development of moorland grasses, these slopes bear practically no representatives of the moorland flora, but are dominated by plants usually found on the arable land. The

soil is honeycombed with puffin burrows, in front of each of which is a pile of droppings. The characteristic smell of such areas suggests irresistibly that the increase of nitrogenous manuring is responsible for the change in vegetation. This plant community is also found, though it is less marked, on the west side of Gleann Mòr, north of the Eriophoretum, and again below the rock known as the Lover's Stone. In each case many puffin burrows are to be found. Smaller isolated patches are scattered all round the low cliffs. The two plants most directly associated with the burrows are *Stellaria media* and a luxuriant form of *Poa annua*. On the island of Dùn the composition of the society is as follows:

Holcus mollis	d.	Festuca ovina	f.
Poa annua	a.	Ranunculus acris	f.
Stellaria media	a.	Potentilla anserina	f.
Rumex acetosa	a.	Angelica sylvestris	o.
Cerastium vulgatum	f.	Montia fontana	r.

No other plants are found on this end of the island and the absence of all moorland species except *Festuca* is very striking. It is quite certain that these areas were never cultivated, but the resemblance between them and the abandoned arable land is very marked, the latter differing in its richer flora. They are described under the moorland because of their obvious development from it, since the land was never tilled, but their superficial affinity is all with the next vegetation to be described. These remarks are based only on direct observation, since the inaccessibility of St Kilda renders experiments over a long period difficult to conduct, but it seems most probable that an example is here afforded of a plant community controlled by the biotic factor of its bird inhabitants. No difference of soil, slope, exposure or history can be discovered which could possibly differentiate the areas in question from similar areas of moorland, except the presence of puffins (compare the north end of Dùn with the peninsula of Ruaival). The rank vegetation round the burrows was noticed by Gibson, who visited the island in 1891 (1).

II. Abandoned arable land.

At their most flourishing period the island population cultivated *some* 50 acres of land situated close to the village, but of recent years they have preferred to obtain what they could from visiting ships, until in the year preceding the evacuation only two or three acres were sown. The method of cultivation was similar to that used in the Outer Hebrides; no horses were available and the effect on the land seems to have been neither deep nor lasting. Fields sown only two years ago now resemble almost exactly those abandoned for many years. A certain amount of manure, in the form of house refuse and probably seaweed, was however incorporated in the soil, and this may be responsible for the resemblance to the puffin colonies described above. The area is dominated by a rank growth of *Holcus lanatus* with a number of attendant species:

Holcus lanatus	d.	Trifolium repens	a.
Ranunculus acris	a.	Potentilla anserina	a.

Cerastium vulgatum	a.	Leontodon autumnalis	o.
Agrostis vulgaris	a.	Pteris aquilina	o.
Anthoxanthum odoratum	a.	Euphrasia vulgaris	o.
Angelica sylvestris	f.	Festuca ovina	o.
Luzula campestris	f.	Prunella vulgaris	r.
Rumex acetosa	f.	Potentilla erecta	r.
R. obtusifolius	f.	Senecio jacobaea	r.
Plantago lanceolata	f.	Vicia sepium	l.f.
Lolium perenne	f.	Achillea millefolium	l.f.
Poa trivalis	f.		

Athyrium filix-foemina occurs in the walls between the plots. In a more southern part of Britain the bracken might be expected eventually to dominate the area, but here it is always small and grows below the level of the *Holcus* inflorescences.

This society covers the ground inside the village wall except for a small portion cut off by the river (Amhuinn Mhòr), and inside all the sheep enclosures (*vide* map). Outside the village wall and on the plateau of An Lag Bo'hn Tuath a gradual transition to the moorland vegetation occurs. This is marked by the mixing of *Holcus*, *Trifolium*, *Rumex acetosa* and *Ranunculus acris* with moorland species, giving a richer and greener turf than is found on the hills. *Rumex acetosella* is commoner here than either on the moorland or on the arable land.

Twelve apparently introduced species are found in the village street and among the houses, but they occur sporadically and play no part in any plant community.

Alopecurus geniculatus	Plantago major
Capsella bursa-pastoris	Polygonum aviculare
Chrysanthemum segetum	Sonchus oleraceus
Cnicus lanceolatus	Triticum repens
C. arvensis	Urtica dioica
Galeopsis tetrahit	Vicia hirsuta

It seems probable that they will in time follow the fate of some formerly recorded arable weeds of which nothing could be found (e.g. *Spergula arvensis*). Curiously enough *Vicia hirsuta* is a new record, but one cannot say whether it was previously overlooked or is a recent immigrant.

Lowland marsh.

As a general rule streams which descend from the hills to the relatively flat arable land are led through it in deep channels lined with stones. This obviates the formation of bogs, which, as has been observed, are found in most flat parts of the island. Occasionally, however, damp marshy areas are found, as along the lower parts of the Amhuinn Mhòr, which are slightly different from the moorland marshes, showing the following characteristic species:

Ranunculus flammula	a.	Iris pseudacorus	f.
Holcus lanatus	a.	Lychnis flos-cuculi	f.
Juncus articulatus	a.	Eleocharis uniglumis	l.f.
Montia fontana	a.	Carex flava	o.
Anagallis tenella	f.	Potamogeton polygonifolius	o.
Carex goodenowii	f.	Trifolium repens	o.
C. stellulata	f.	Angelica sylvestris	r.
Eriophorum angustifolium	f.	Epilobium palustre	r.
Hydrocotyle vulgaris	f.	Sagina procumbens	r.

This community is also developed around the foot of Gleann Mòr, on the rocks where its streams fall into the sea. Here, and in the peaty pools above, *Callitriche stagnalis* is found. Its absence from the southern side of the island is remarkable.

This marsh vegetation stands in the same relation to the arable land as the vegetation of the hillside bogs does to the moorland. Many species of arable land are found mixed with the marsh plants.

III. MARITIME VEGETATION.

This may conveniently be divided into three communities:

(*a*) Littoral vegetation.
(*b*) Vegetation of low cliffs.
(*c*) Vegetation of moorland affected by sea spray.

(*a*) *Littoral vegetation.*

The algal flora of the exposed rock faces is poorly developed, probably on account of the violence with which the Atlantic swell strikes the rocks at all times of the year. In sheltered places, however, as in straits between stacs and larger islands, the following zonation was observed:

(1) Submerged even at low tide: *Alaria esculenta, Laminaria saccharina, Himanthalia lorea.*

(2) *Gigartina mamillosa.*

(3) *Fucus platycarpus, Porphyra laciniata.*

(4) *Fucus ceranoides, Porphyra laciniata.*

In pools of brackish water above these communities *Enteromorpha* sp. predominated.

As the rocks become more and more exposed on passing out of a sheltered area, the middle zones disappeared first, the lines of *Alaria* and *Porphyra* persisting almost everywhere, though separated by a wide expanse of bare rock on the open coast.

(*b*) *Vegetation of low cliffs.*

As in the case of the high cliffs, the vegetation consists of fragments of surrounding societies with the addition of certain characteristic plants, viz.:

Cochlearia anglica	a.	Ligusticum scoticum	l.f.
Matricaria maritima	a.	Atriplex babingtonii	o.
Armeria vulgaris	f.	Cerastium tetrandrum	a.
Silene maritima	f.		

When puffin colonies adjoin the low cliffs, as on Dùn, *Holcus mollis, Stellaria media* and *Rumex acetosa* are also found. In regions close to moorland however, as on Ruaival, salt-tolerant species of the moorland flora abound on ledges, e.g. *Plantago maritima, P. coronopus, P. lanceolata, Festuca ovina, F. rubra.*

(c) Moorland areas affected by sea spray.

Where the moorland descends to within a few hundred feet of the sea, a very well-marked community appears, consisting of a few plants of the ordinary flora which are presumably salt-tolerant. This is found in the peninsulas of Ruaival and Gob na h'Airde, on the slopes of the west coast, and to a slight extent round the foot of Gleann Mòr. In all other places the height of the cliffs seems to protect the moorland from the influence of the sea. It must of course be remembered that in winter storms the waves strike the rocks with extreme violence; they have been observed to break right over the island of Dùn, which is 200 ft. above sea-level at its lowest point. This community is dominated by *Plantago maritima*, which in places forms a pure sward. The fine leaves of this and *Statice* give a smooth, even appearance to the vegetation, comparable to good grass turf.

Plantago maritima	d.	Sagina procumbens	f.
P. coronopus	a.	Carex oederi	o.
Festuca ovina	a.	Juncus lamprocarpus	o.
Statice armeria	e.	Agrostis vulgaris	o.
Plantago lanceolata	f.	Euphrasia vulgaris	r.
Carex goodenowii	f.	Cerastium vulgatum	r.
Leontodon autumnalis	f.		

CONCLUSION.

The ecological interest of Hirta in the St Kilda group lies principally in the return of the vegetation to a natural state owing to the removal of the factors of grazing and cultivation. These have not yet had time to take effect, but it seems likely that a considerable development of *Calluna vulgaris* and other heath shrubs will occur in the formerly grazed areas. The moorland grasses will probably diminish, resulting in a decrease of the value of the land as sheep pasture. In the cultivated area, since little or no difference is apparent between areas abandoned two years ago and those which have been left uncultivated for fifty years, no rapid changes can be expected. Most probably some modification of the moorland will establish itself.

The vegetation of areas affected by sea spray and by puffin colonies is described, and an analysis of the composition of the moorland flora given. Attention is drawn to the effect of the puffin colonies on the flora, as an example of the operation of a somewhat rare biotic factor.

My thanks are due to Dr H. Godwin for assistance with this paper, and to Mr R. A. Buckingham for the map.

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COLONISATION BY *EPILOBIUM ANGUSTIFOLIUM*

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An interesting case of colonisation by *Epilobium angustifolium* has recently occurred at Rothamsted. An area of grassland which has been under experiment since 1856 is divided into a number of plots which are annually treated with various combinations of fertilisers, one half of most plots now receiving regular dressings of lime in addition. This treatment has brought about radical changes in the yield and composition of the herbage, which is mown twice a year and never grazed.

The plots continually receiving nitrogen as sulphate of ammonia, with or without mineral fertilisers, have become very acid, a fact which is reflected in the predominance of *Holcus lanatus, Anthoxanthum odoratum* or *Festuca duriuscula* according to treatment, the general tendency being for these grasses to occur in tufts instead of as a uniform herbage.

The winter of 1928–9 was characterised by severe frost, followed during the spring and summer by exceptional drought. Under these abnormal conditions the herbage of the unlimed parts of all plots receiving sulphate of ammonia was practically devastated, and the surface of the ground was covered with a mat of decaying vegetation. Recovery was very slow, and it was not until the autumn of 1931 that the herbage on these plots again reached its normal density. In the process of recovery certain changes in composition occurred as a result of the unusual opportunity for colonisation afforded by the less acute competition, the most prominent invader being *Epilobium angustifolium*. In the presence of continued sulphate of ammonia and superphosphate the normal herbage consists chiefly of clumps of *Festuca duriuscula* and *Anthoxanthum odoratum*, with considerable areas of bare ground between, which are covered with a form of dry peat consisting of incompletely decayed dead leaves. Where complete minerals (superphosphate, potash, etc.) are used in conjunction with heavy dressings of sulphate of ammonia the dominant species is *Holcus lanatus*, which also grows in tufts and covers the surrounding bare spaces with a peaty layer of dead leaves. In this case, however, numerous *Holcus* seedlings may spring up on the peat, and in some seasons these are able to establish themselves and cover the area more effectively.

During the process of recovery since 1929, the herbage has resumed its normal *facies* in the main but, when superphosphate only is associated with the sulphate of ammonia, large quantities of *Epilobium angustifolium* have established themselves in the bare spaces between the clumps of grass. When complete minerals are present much less *Epilobium* has obtained a footing. In the latter case the actual opportunity for colonisation was in reality greater, owing to the proximity of large quantities of the invading species just beyond the boundary line within ten yards of one of the plots, whereas that receiving

superphosphate was much farther away, at a distance of sixty yards from the nearest centre of infection[1].

Tests were made to ascertain if the selective colonisation by *Epilobium* under these conditions was due to a difference in the hydrogen-ion concentration of the soil, determinations being made both on the peaty surface layer and the underlying soil of all three plots. The hydrogen-ion concentration of the underlying soil was remarkably uniform, only varying between 3·7 and 4·0, but the pH value of the peat layer ranged over wider limits, tending to be somewhat higher, as is shown in Table I.

Table I.

Plot	Manuring	Soil	pH values			
4²	Sulphate of ammonia + superphosphate	Peaty layer	4·2	5·6	4·2	4·8
		Lower ,,	4·0	4·0	<3·8	4·0
9	Sulphate of ammonia + complete minerals	Peaty layer	4·6	4·1	4·2	—
		Lower ,,	4·0	4·0	4·0	—
11¹	Extra sulphate of ammonia + complete minerals	Peaty layer	4·0	4·0	4·0	—
		Lower ,,	<3·8	<3·8	4·0	—

Further samples were taken to determine whether the distribution of *Epilobium* on the bare spaces was associated with differences in pH, and comparison was also made with the soil from the "mother" areas beyond the boundary line.

Table II.

	pH values				
Bare spaces on plot 4², *with Epilobium*	4·2	4·2	4·0	4·0	4·1
,, ,, *without* ,,	5·2	4·4	4·2	4·1	4·1
Soil from "mother" area of *Epilobium*	4·5	4·5	4·6	5·0	4·8

The range of hydrogen-ion concentration of the soil on which *Epilobium* grows freely is as wide as that where it has not established itself, and therefore the assumption is ruled out that this species is particularly favoured by acid soils, but will not grow so freely in less acid situations.

The varying distribution would appear to be a question of competition rather than soil reaction. Where most *Epilobium* has sprung up the return of the normal vegetation on the devastated patches has been less complete than on the other plots, and the young *Epilobium* seedlings had therefore a better chance of establishing themselves. This fits in with the known facts of the habits of the species, which tends to spring up freely where areas have been cleared by fire, blizzard or similar drastic agencies, to disappear again as other vegetation reasserts itself.

No attempt has been made to eliminate the invading *Epilobium* nor to prevent it from seeding, but careful watch will be kept on its behaviour during the next few years.

October, 1932. During the present season, since the above was written, much less *Epilobium* has appeared, thus supporting the idea that competition was the determining factor.

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[1] These remarks do not apply to the *limed* areas on which the devastation of the herbage did not occur.

THE WEED SEED POPULATION OF ARABLE SOIL

II. INFLUENCE OF CROP, SOIL AND METHODS OF CULTIVATION UPON THE RELATIVE ABUNDANCE OF VIABLE SEEDS

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(With four Figures in the Text.)

CONTENTS.

I. INTRODUCTION.

IN a previous number of this JOURNAL[1] an account was given of an attempt to make a quantitative estimate of the number of viable weed seeds buried in the soil of Broadbalk wheat field, Rothamsted, in 1925, the influence of manuring on the distribution and the relative lengths of dormancy of the various species

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[1] **Brenchley, W. E. and Warington, K.** "The weed seed population of arable soil. I. Numerical estimation of viable seeds and observations on their natural dormancy." This JOURN. **18**, No. 2, 235–72, 1930.

also being considered. At that time the weed flora was so prolific as to be a serious menace to the wheat crop, which, for experimental reasons, has been autumn sown on the same area since 1843. A definite campaign against the weeds was therefore planned, but, as it was undesirable that any break in crop continuity should occur, it was decided to make an intensive attack on one part of the field by means of fallowing operations for two years, while the rest of the area was cropped and subjected to as thorough cultivation as was possible under the circumstances. At the end of the two years the process was reversed, but the fallowed portions were arranged to overlap, so that one part of the field remained without a crop for four years. At the same time a parallel experiment was carried out at Woburn on sandy soil on continuous wheat and barley plots to provide a comparison between the effects of fallowing on different types of soil. The data for this latter experiment are now available and, before proceeding to deal with the effects of fallowing operations, it is necessary to consider briefly the weed seed population of the Woburn soil at the beginning of the experiment, for comparison with the Rothamsted results set forth in the previous paper.

II. Buried weed seeds in Woburn soil, under continuous wheat and barley.

Stackyard field, Woburn, carried wheat and barley continuously from 1877 to 1926 inclusive, when the land had become so foul with weeds that it was decided to put it under bare fallow for two years. In 1929 the field was again under crop.

The wheat is always autumn-sown, necessitating autumn ploughing only, followed by cultivating and hoeing as occasion arises. The barley is always spring-sown, permitting both autumn and spring ploughing. So far as cultivation goes, the barley crop has allowed greater opportunities for the germination and destruction of weed seedlings, such as *Alchemilla arvensis*, *Cerastium vulgatum*, *Juncus bufonius*, *Matricaria inodora*, *Myosotis arvensis* and *Vicia hirsuta*. On the other hand, the wheat, established in the autumn and spreading its tillers early in the year, has probably reduced by competition some species that are able to grow and hold their own with spring-sown barley, such as *Capsella bursa-pastoris*, *Chenopodium album*, *Gnaphalium uliginosum* and *Veronica buxbaumii* (*V. polita* of preceding paper[1]). To a less marked extent this reduction among wheat applies to the more abundant weed, *Spergula arvensis*. The relative abundance of the major weed species among the two crops is shown in Table I, all minor species, of which less than twenty appeared from the bulked samples in both crops, being omitted.

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[1] Since the publication of the first paper, Dr Eric Drabble has examined specimens of the *Veronica polita*, which had been considered to be a probable hybrid between *V. polita* and *V. buxbaumii*, and we are indebted to him for his opinion that the species is in reality true *V. buxbaumii*. In future, therefore, the name *V. buxbaumii* will be used for this species.

Table I. *Woburn soil. Number of seedlings from buried seeds present before fallowing, all samples added together*.* (8⅔ *sq. ft. area.*)

	Wheat	Barley
Species predominant in wheat		
Agrostis stolonifera	181	86
Alchemilla arvensis	4,520	44
Arenaria serpyllifolia	84	6
Cerastium vulgatum	435	1
Juncus bufonius	339	8
Legousia hybrida	60	23
Matricaria inodora	3,183	234
Myosotis arvensis	87	—
Papaver spp.	131	4
Poa annua	2,816	1,314
Veronica arvensis	407	137
V. hederæfolia	48	1
Vicia hirsuta	130	—
Viola arvensis	116	13
	Total 12,537	Total 1,871
Species predominant in barley		
Capsella bursa-pastoris	255	1,520
Chenopodium album	7	162
Gnaphalium uliginosum	344	1,007
Lamium amplexicaule	70	185
Polygonum aviculare	1,041	1,316
P. convolvulus	10	30
Rumex acetosella	43	56
Senecio vulgaris	39	84
Spergula arvensis	8,475	16,110
Stellaria media	280	915
Veronica buxbaumii	14	860
Total, excluding Spergula arvensis	2,103	6,135
Spergula arvensis	8,475	16,110
Grand total	10,578	22,245

* Twenty-six barley soil samples, each 48 sq. in. area (8⅔ sq. ft.). Twenty-two wheat soil samples, each 48 sq. in. area (7¼ sq. ft.). For purposes of comparison with barley the wheat weed seeds were recalculated for an area of 8⅗ sq. ft.

A further analysis of Table I shows very clearly how the weed flora associated with a particular crop is influenced by the correlation between the periodicity of germination of the various weed species and the method of cultivation and time of sowing of the crop (Table II).

Species with maximum germination in autumn are able to maintain their position with autumn-sown *wheat*, but are ruthlessly cut down, often before flowering, by the later ploughing and cultivating for the spring-sown *barley*. Those weeds that show no periodicity, and yet are chiefly associated with wheat, have generally some peculiarity which explains the distribution. *Matricaria inodora* is very impatient of competition and usually occurs in abundance only in thin places and at the edges of crops. The seedlings which appear with the wheat in autumn get well established and doubtless, on this sandy soil on which the wheat crop is not very heavy, they are able to hold their own when spring growth begins. With the barley crop, on the other hand, the *Matricaria* seedlings come into direct competition at a very early stage, and the species

has gradually been crowded out by the repeated growth of the same crop. With regard to *Agrostis, Vicia* and *Juncus*, it may be that a long growth period is needed before seed formation occurs, and that seeds have time to ripen with the wheat but are not fully developed by the time the spring-sown barley crop is harvested. *Poa* and *Arenaria* grow freely during the autumn and winter months, producing plants that with wheat are able to seed and restock the soil, but with barley are cut down by cultivation. Probably both species suffer from the competition of a strongly growing cereal crop, so that in spite of their ability to germinate throughout the year, comparatively few plants are able to establish themselves from seeds which start into growth in the spring.

Table II. *Periodicity of germination of major weed species.*

A. Species dominant in wheat.

Maximum germination in *autumn**	No peak season for germination
Alchemilla	Agrostis
Cerastium	Arenaria
Legousia	Juncus
Myosotis	Matricaria
Papaver	Poa
Veronica arvensis†	Vicia
V. hederæfolia	
Viola	

B. Species dominant in barley.

Maximum germination in *winter* and *spring*	No peak season for germination
Polygonum aviculare	Capsella
P. convolvulus	Chenopodium
	Gnaphalium
	Lamium
	Senecio
	Spergula
	Stellaria
	Veronica buxbaumii†

* For convenience of reference autumn implies October–December, winter implies January–March, spring implies April–June, summer implies July–September.

† At Rothamsted also *Veronica arvensis* and *V. hederæfolia* are correlated with continuous wheat, and *V. (buxbaumii) polita* with continuous barley.

The species dominant with *barley* are equally definite. No dominant weeds occur whose maximum germination is in autumn, as the bulk of their seedlings are cut down before the crop is sown. *Polygonum aviculare* and *P. convolvulus* are late germinating species, plentiful in both crops, but probably somewhat reduced in wheat by competition due to the greater development of the crop at the normal time of germination of the weed. The species with no definite periodicity are less easy to account for, unless it is they are more susceptible to competition at the time that the wheat is covering the ground with its tillers, while the barley is yet too small to be a serious competitor. In this case there is no definite, clean-cut factor, such as ploughing, to cause a sweeping reduction of any species among wheat as compared with barley, and this is shown by the number of weed seeds present on equal areas. Whereas the species

dominant in wheat gave 12,537 seedlings in wheat against 1,871 in barley, those dominant in barley gave 6,135 in barley against 2,103 in wheat, *Spergula* being omitted in both cases.

It is advisable to exclude *Spergula* in making the comparison, as it is so abundant in both crops that it swamps the other species collectively, and might be suspected of masking the true result. This, however, is not the case, as no alteration is brought about by its inclusion.

III. Influence of methods of cultivation on the weed seed population of soil.

Soil samples were taken annually, both at Rothamsted and Woburn, the procedure and method of after-treatment being fully described in the previous paper (pp. 238–40). Complete data for the Rothamsted area are now available as to the effect of the first and second years' fallowing as contrasted with the improved cultivation of the cropped portion. In the case of Woburn the whole field was put under fallow, so no comparison with crop cultivation is possible, attention being therefore confined to the results of fallowing. From the ecological point of view the interest lies in the varying response of the different species to the two forms of human interference with their natural habitat.

When land is deliberately left fallow in order to reduce weed infestation, the chief aim is to encourage germination of the buried weed seeds, and to cut down the seedlings before any have developed far enough to flower and produce more seed to re-infest the soil. This entails repeated working of the ground at intervals which vary according to the seasonal conditions prevailing. At the same time, these cultivations tend to bring fresh supplies of seed nearer to the surface and into conditions favourable for germination. It has become evident that the *crux* of the situation lies in the length of time between cultivations; since for certain weeds, under certain seasonal conditions, the period of safety is far less than is usually reckoned. For a clearer understanding of this point in its relation to individual species, it may be useful to summarise here (Table III) the processes of cultivation on the cropped and fallowed parts of Broadbalk Field at Rothamsted during this period of the experiment. Table III has general reference to sections 1, 2 and 3, in conjunction with which it should be read.

The numbers of viable seeds vary so greatly, both from species to species, and from plot to plot for any one species, that it is difficult to follow the trend of events if the actual totals only are considered. For purposes of comparison these total figures have been recalculated to a basis of 100 of the seeds present in the soil at the beginning of the experiment, i.e. really on a percentage basis, but the actual figures are also given in any tables utilised.

The experiment under discussion provides data as to the varying response of different weed species to identical fallowing treatment, and also affords a comparison of the effect of cropping and fallowing on the same species. For

the sake of clarity these two points will first be dealt with separately and summarised together at a later stage.

Table III. *Broadbalk Field cultural operations, 1925–7.*

1925	Fallowed, top three-fifths	1925	Cropped, bottom two-fifths
Oct. 28–Nov. 13	Ploughed	Oct. 28–Nov. 13	Ploughed with tractor
		Nov. 24	Drag harrowed
		Nov. 25	Wheat drilled, harrowed after
1926		**1926**	
Feb.	Furrows turned back		
		March 17	Began to harrow out grass
April 20	Disc harrowed	April 15	Hoeing begun with "Planet" cultivator and continued when possible
May 25, 26	Disc harrowed both ways		
June 1	Cross cut with path hoe (like a broadshare)	June 3	Thistles pulled up after rain
June 15, 19	Cross ploughed (horses)		
July 26, 31	Tractor cultivated both ways		
Aug. 4	Thistles cut with thistle bar and tractor	Aug. 26	Wheat cut
Aug. 5	Harrowed		
		Sept. 9	Wheat carted
Sept. 29–Oct. 4	Ploughed landways	Sept. 29–Oct. 4	Ploughed
Oct.	Thistles cut	Oct. 8	Worked down and wheat drilled
1927		**1927**	
Feb. 1	Cross-ridged, completed March 3		
March 29	Started splitting ridges, completed April 6	March 22	Wheat harrowed
		April 21	Horse hoed
May 14	Split ridges again, completed May 17	May 5	Began hand hoeing
May 20	Harrowed down ridges, completed May 23		
June 23	Ploughed across the plots and finished July 9		
Aug. 4, 5	Disc harrowed	Aug. 26–27	Wheat cut
Aug. 6	Thistles cut with thistle bar and tractor		

(1) *Response of different species to identical fallowing.*

(a) Rothamsted wheat.

The effect of fallowing on the weed seed population of the soil is really the result of a single factor, i.e. human interference with seedlings which have not been allowed to flower and develop seeds. If fallowing is efficiently carried out every germinating seed is put out of action, and the degree of reduction depends upon the proportion of the seed population which is brought into a favourable position for germination during the process of cultivation. The seeds which are still in a naturally dormant condition will not germinate, even when thus favourably placed, and the varying response of different weed

species to fallowing is chiefly due to the variation in their period of natural dormancy. If, however, fallowing is not properly carried out, or if the period between cultivations is too long, certain of the seedlings in some species may develop far enough to produce seeds which aid in re-stocking the soil, thus vitiating the beneficial effects of the fallow for those species.

The simplest way to demonstrate the very variable response of different species is to arrange them in numerical order of response per 100 seeds present before fallowing.

Table IV. *Number of viable buried seeds from equal areas in three successive years. (All seven plots together.)*

Land cropped 1925, fallowed 1926, 1927.

	Actual population per 21 sq. ft.			Relative population in percentages		
	1925	1926	1927	1925	1926	1927
Group A						
Capsella bursa-pastoris	222	243	216	100	109	97
Arenaria serpyllifolia	381	400	350	100	105	92
Veronica buxbaumii	117	123	75	100	105	**64**
Group B						
Veronica hederæfolia	916	712	375	100	78	41
Papaver rhœas	44,564	28,143	20,489	100	63	46
Group C						
Matricaria inodora	127	67	45	100	53	35
Linaria minor	201	105	54	100	52	27
Legousia hybrida	658	322	250	100	49	38
Euphorbia exigua	353	172	35	100	49	**10**
Veronica arvensis	3,221	1,541	687	100	48	21
Alchemilla arvensis	5,658	2,463	1,799	100	43	32
Group D						
Bartsia odontites	128	51	41	100	40	**32**
Sonchus arvensis	125	47	24	100	38	19
Myosotis arvensis	774	281	135	100	37	17
Caucalis arvensis	275	101	41	100	37	15
Group E						
Galium tricorne	66	20	6	100	30	9
Atriplex patula	452	130	53	100	29	12
Polygonum convolvulus	42	12	1	100	29	2
Senecio vulgaris	372	103	28	100	28	7
Æthusa cynapium	283	70	23	100	25	8
Medicago lupulina	153	38	10	100	25	7
Polygonum aviculare	1,130	275	43	100	24	4
Anagallis arvensis	95	22	26	100	23	**27**
Alopecurus agrestis	5,440	1,224	240	100	22	4
Scandix pecten	604	111	20	100	18	3
Stellaria media	104	16	11	100	15	11
Galium aparine	243	34	20	100	14	8

The species are arranged in order of the reduction undergone during the first year's fallowing. Those in heavy type in the last column are species which behaved abnormally for their group in the second year's fallowing.

After a single year's fallowing the remaining viable seeds present varied from 109 per cent. to 14 per cent. of the original numbers, a second year's fallowing reducing these to from 97 per cent. to 2 per cent. The further re-duction in the second year averaged about 20 per cent., with a few noteworthy

exceptions, which are clearly seen if the species are grouped, as in Tables IV and V.

Table V. *Summary of effect of fallowing on percentage of buried weed seeds.*

After one year's fallow	After two years' fallow
Group A. Over 100%	100–90 %, except *Veronica buxbaumii* 64 %
„ B. „ 61–80 %	41–50 %
„ C. „ 41–60 %	21–40 %, except *Euphorbia exigua* 10 %
„ D. „ 31–40 %	13–20 %, except *Bartsia odontites* 32 %
„ E. „ 10–30 %	12 % and below, except *Anagallis arvensis* 27 %

Group A. The most unexpected result was the behaviour of *Capsella, Arenaria* and *Veronica buxbaumii* in keeping up their numbers in spite of the frequent disturbance of the soil, but an adequate reason is revealed by a correlation of the habits of the species and the cultural operations carried out. *Arenaria* and *V. buxbaumii* are characteristically trailing species that begin to flower and fruit at a very early stage, comparatively soon after germination. As they continue flowering over a long period the soil is freely replenished with seed. The importance of the insignificant, earliest formed flowers has never yet been fully appreciated, but it is now becoming evident that this neglected habit is at the bottom of many failures to reduce weeds by methods of cultivation. *Capsella* is not obviously of the same type, but under certain conditions it behaves very similarly. Many plants will produce large rosettes of leaves and delay flowering till they are thoroughly well established. On the other hand, search among *Capsella* colonies, particularly during the winter months, reveals numerous tiny plants, perhaps only half an inch high, flowering and producing seed at a very early stage in their life history. In the previous paper[1] it has already been shown that these three species germinate freely during the winter months. *Capsella* germinates readily all the year round with a certain maximum in the spring, *Veronica buxbaumii* also germinates at any time, without any peak period, whereas *Arenaria* comes up freely in winter and spring, very few seedlings appearing in the summer. An examination of Table VI shows various undisturbed periods when the land was under fallow during which it would have been possible for these species, with their particular habits of growth and germination, to replenish the soil with seed.

It is probable that the danger point for these species is the long slack period from October or November to March or April, when those in charge of farm operations would not be expecting that any plants would be sufficiently active in seed formation to do any damage.

The winter period, October to April, was particularly favourable in 1925–6, as the mean temperature in every month exceeded the average of that for the 53 years 1878–1930 (Table VII). The following winter the mean temperature

[1] **Brenchley, W. E.** and **Warington, K.**, This JOURN. **18**, No. 2, 235–72, 1930.

equalled the average, and the relative mildness of both seasons was doubtless favourable to the germination and growth of the species under discussion.

Table VI. *Fallowing operations on Broadbalk Field.*
Intervals between cultivations.

1st year	Nov. 13, 1925–Feb. 1 (or later), 1926	...	...	80 days at least
	Feb. 15 (approx.)–April 20...	...	...	64 days approx.
	April 20–May 25	...		35 days
	June 19–July 26	...		37 days
2nd year	Oct. 4, 1926–Feb. 1, 1927 ...	...	...	120 days
	March 29–May 14	...		46 days
	June 23–Aug. 4	...		42 days

Table VII. *Mean monthly temperatures.*

	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	Mean
1925–6	50·3	43·9	42·1	38·2	44·0	43·2	48·0	44·2
1926–7	50·3	38·8	36·3	38·7	38·1	44·6	45·8	41·8
Average 1878–1930	48·7	42·1	38·5	37·5	38·5	41·1	45·4	41·7

The reduction in *Veronica buxbaumii* which occurred after the second year's fallow may be associated with its very short period of natural dormancy. Under favourable conditions practically all the seeds will germinate at once, and if a high germination happened to be induced shortly before a cultivation the number of potential seed producers would be greatly reduced, without others being in waiting to take their place. This may also have happened sometimes during the 1926–7 season, but as *Capsella* and *Arenaria* have much longer periods of natural dormancy, preventing such a large proportion of seeds from germinating at once, this particular factor would not operate to reduce them to the same degree.

Group B. Veronica hederafolia is another trailing species which begins to form fruit at a very early stage. Under normal conditions its germinating period is practically confined to the autumn, and a fair proportion of seeds appear to have a period of more than three years' natural dormancy. The marked autumn periodicity, coupled with the slackness in cultivation during the winter months, obviously permitted a certain amount of re-stocking of the soil with seeds, thus accounting for the comparatively small reduction to 78 and 41 per cent. effected by fallowing from year to year.

Papaver rhœas comes in an entirely different category, as flowering and seed production is always delayed till late spring or early summer, although seeds may germinate freely from autumn to spring according to climatic conditions. This habit of flowering subjected *Papaver* to the full force of spring and summer cultivation, so that no opportunity occurred for re-stocking the soil with fresh seed. The slow reduction to 46 per cent. in two years effected by fallowing in this case must therefore be attributed to the long period of natural dormancy in this species. Under experimental conditions in germination pans, where a small volume of soil is thoroughly turned over eight times a year,

poppies are still germinating at the present time (1931) in samples taken in August, 1925. This fully accounts for the failure of even prolonged fallowing to bring about any adequate reduction of poppies on badly infested land, as the remaining seeds which gradually emerge from dormancy very soon recolonise the land, owing to the prolific seed production per plant. From the practical point of view it is evident that fallowing is an uneconomic means of eradicating poppies, and other methods need to be sought to combat them.

Group C. The species in this group, except *Euphorbia exigua*, show a medium response to fallowing, about one-third of the original seed stock being left after two years' treatment. *Legousia, Linaria* and *Matricaria* are all species which delay flowering until spring or summer and are therefore affected by cultural operations. The relatively long period of dormancy in *Legousia* and *Matricaria*, as contrasted with the short period in *Linaria*, is reflected in the difference in the ultimate reduction of the three species to 38, 35 and 27 per cent. respectively.

Alchemilla and *Veronica arvensis* are more difficult to reconcile with this group, as they might have been expected to be more resistant to the influence of fallowing. Both germinate chiefly in autumn, both are of the trailing habit which may begin to fruit before spring cultivation becomes active, and both have relatively long periods of natural dormancy, all of which are factors tending to keep up the seed population of the soil. Closer observation of the habits of these two species in the field is needed, as it is possible that in spite of their habit they may delay flowering till spring or summer, or may be unable to ripen seed from the earliest formed flowers. The discrepancy in behaviour between the three species of *Veronica* is very marked, *V. arvensis* being so reduced by fallowing that it is almost on the border line of the lower group D.

Euphorbia exigua is the one member of this group which shows further rapid response during the second year's fallowing, being reduced to 10 per cent. of the original population. This is probably associated with the very short period of natural dormancy of the majority of seeds of this species, coupled with the habit of summer flowering. It is recognised (previous paper, p. 256) that *E. exigua* tends to be irregular in its habit of germination, which may be delayed so as to give a bigger rush of seedlings in the second year than in the first from the same samples of soil. It would therefore be unwise to assume that the drastic reduction here recorded would always occur with this species under similar treatment in different seasons. Further information on this point will probably emerge from the present experiment as time goes on.

Group D. Species in groups D and E, with the solitary exception of *Bartsia odontites*, may be regarded as being effectively reduced by fallowing operations.

Sonchus, Myosotis and *Caucalis* are all spring or summer flowering, with a fairly wide periodicity of germination, and the two former have only short periods of natural dormancy. *Caucalis* is very efficiently reduced considering that its natural dormancy is rather long.

Bartsia odontites, in spite of its heavy reduction during the first year, was little affected in the second season. This was surprising in view of the apparent short period of natural dormancy determined during the preliminary experiment, but there is now some evidence from later observations that *Bartsia* is erratic in its germination and may vary in the length of its natural dormancy. If so, it may have happened that seasonal conditions during the second year of fallowing were unfavourable to the germination of this species and that most of the seeds remained dormant, keeping up a relatively high level of soil population. Under other seasonal conditions *Bartsia* might have come into line with the other species of this group.

Group E. Nearly half of the more abundant weeds fall into this category, including some of the most troublesome species, such as *Alopecurus*. The peak period of germination varies considerably within the group, but with the two exceptions of *Stellaria* and *Senecio* all are plants which normally flower in spring and summer and are, therefore, open to influence by cultivation. In the majority of cases the period of natural dormancy is short, and this fact, coupled with the incidence of flowering, results in a fairly complete clearance of viable seeds from the soil during two years' continuous fallow.

Anagallis arvensis is the only species in which no further reduction was effected by the second year of the fallow, which was doubtless partly due to the long period of natural dormancy preventing so thorough a clearance. Some other factor also appears to have operated here, as this is the only instance where no reduction at all occurred in 1927. The possibility exists that seasonal conditions in this year were very favourable to the rapid germination and growth of *Anagallis*, so that it was able to set seed and replenish the soil in the interval between cultivations, particularly from March 29th to May 14th. The records, however, show nothing abnormal in the weather conditions at this time, as average conditions of temperature, rainfall and bright sunshine were prevailing. Soil replenishment might also have happened between June 23rd and August 4th, except that summer germination is abnormal, though some climatic factor might have induced it on this occasion. Though average temperatures prevailed, this period was very deficient in bright sunshine and the rainfall was rather above the mean for 78 years, which may have been a combination of circumstances favourable to this species.

Stellaria and *Senecio* will germinate freely all the year round, though *Senecio* tends to a maximum peak in spring. Both plants, likewise, flower and fruit to some extent at all seasons, but the seeds have very short periods of natural dormancy. Consequently when a good seed bed is produced by fallowing the bulk of the seeds germinate soon after they are shed, and as this happens more rapidly during the spring and summer the numbers destroyed by cultivation far exceed those replaced in the soil during the slack winter period. The short period of dormancy is the critical factor, as with constant cultivation and induced rapid germination, relatively few seeds are left to carry out recolonisa-

tion, and this much more than counter-balances the number added by winter flowering plants.

(b) *Woburn wheat and barley.*

It was originally intended to treat these plots in exactly the same way as at Rothamsted and to fallow them intensively for two seasons, but owing to unavoidable circumstances no cultivations were carried out between January and July in the second year. This to a large extent minimised the value of the fallow from an agricultural point of view, but provided a most practical object lesson on the rapidity with which certain species will recolonise cleared land, unless active repressive measures are maintained against them. The longest intervals between the cultivations of the Woburn barley plots are set out in Table VIII, those for wheat being much the same, varying by a few days only.

Table VIII. *Fallowing operations in Stackyard Field, Woburn. Prolonged intervals between cultivations on barley plots.*

March 10–May 17, 1927	68 days
August 22–November 2, 1927	72 days
January 9–July 6, 1928	179 days

Table IX. *Number of viable weed seeds from equal areas in three successive years (Woburn). (All plots together.)*

Land cropped 1926; fallowed 1927, 1928.

	Actual population per 8⅜ sq. ft.						Relative population in percentages					
	Wheat			Barley			Wheat			Barley		
	1926	1927	1928	1926	1927	1928	1926	1927	1928	1926	1927	1928
Group A												
Myosotis arvensis	87	103	39	—	1	—	100	118	45	—	—	—
Alchemilla arvensis	4,520	4,197	3,271	44	11	27	100	93	72	100	25	61
Papaver spp.	131	110	70	4	12	12	100	84	53	—	—	—
Group B												
Legousia hybrida	60	41	24	23	34	13	100	69	39	100	148	57
Veronica hederæfolia	48	30	95	1	—	3	100	61	195	—	—	—
Group C												
Viola arvensis	116	67	52	13	16	13	100	58	45	—	—	—
Arenaria serpyllifolia	84	47	65	6	3	8	100	56	77	—	—	—
Veronica arvensis	407	200	161	137	12	28	100	49	40	100	9	20
Spergula arvensis	8,475	3,967	3,470	16,110	7,389	4,767	100	47	41	100	46	30
Matricaria inodora	3,183	1,462	1,216	234	99	63	100	46	38	100	42	27
Agrostis stolonifera	181	79	143	86	41	131	100	44	79	100	48	152
Juncus bufonius	339	145	427	8	2	25	100	43	126	—	—	—
Group D												
Gnaphalium uliginosum	344	110	96	1,007	106	190	100	32	28	100	11	19
Group E												
Cerastium vulgatum	435	125	181	1	—	2	100	29	42	—	—	—
Poa annua	2,816	720	771	1,314	396	1,019	100	26	27	100	30	78
Stellaria media	280	72	158	915	335	435	100	26	57	100	37	48
Vicia hirsuta	134	32	38	—	—	—	100	24	28	—	—	—
Veronica buxbaumii	14	12	9	860	228	211	—	—	—	100	27	25
Capsella bursa-pastoris	255	33	70	1,520	523	535	100	13	27	100	34	35
Rumex acetosella	43	4	7	56	2	2	100	8	17	100	4	4
Senecio vulgaris	39	2	4	84	17	28	100	6	9	100	20	33
Lamium amplexicaule	70	4	8	185	50	32	100	5	12	100	27	17
Polygonum aviculare	1,041	37	119	1,316	42	104	100	4	11	100	3	8
Chenopodium album	7	—	1	162	25	34	—	—	—	100	15	21

In Table IX the Woburn weed species are arranged in the order in which they were affected by the first year's fallowing on the wheat land, which carried more weeds than the barley soil, *Spergula* being excluded. For convenience of reference the species are grouped according to the percentage of buried seeds remaining at the end of the year, as follows:

Group A. Over 80 %   Group C. 41–60 %
  ,,   B. 61–80 %   ,,   D. 31–40 %
            Group E. 0–30 %

These groups correspond to those on Rothamsted soil, except that group A ranges from 80 per cent. instead of 100 per cent. upwards, and group E extends below the 10 per cent. of the parallel Rothamsted group.

The comparisons emerging from this table are dealt with under the following headings, (α), (β) and (γ).

(α) *Effect of first year's fallow on Woburn wheat and barley land.* Several species which are prominent on the wheat plots are either absent from the barley plots or are there present in such small numbers that the percentage figures are entirely meaningless and are therefore omitted. Only with *Chenopodium album* and *Veronica buxbaumii* did the reverse position occur.

In all species of which the seeds were initially present in any abundance the reduction due to fallowing was practically equal on the wheat and barley soil. *Spergula, Matricaria, Agrostis, Poa, Polygonum aviculare* and probably *Stellaria* come into this category, which also includes *Rumex acetosella* in spite of its small numbers. Wherever discrepancies occur it will be noticed that relatively few seeds were present on one or other of the soils, in which case the reduction was usually greater, as with *Alchemilla, Veronica arvensis, Capsella, Senecio* and *Lamium amplexicaule*. *Gnaphalium,* however, showed the greater reduction on the barley soil which originally contained the most seeds, and with *Legousia* there was a reduction on the wheat soil and an increase on the barley soil, which is not easy to explain.

(β) *Comparison of effect of first year's fallow on Rothamsted and Woburn wheat soil.* At Rothamsted fallowing operations began with the first ploughing in October, but at Woburn the land was left untouched until January, a procedure which had a marked influence on the comparative reduction of certain species. At Rothamsted *Capsella, Arenaria* and *Veronica buxbaumii* reaped the advantage of the long quiescent winter period which afforded opportunity to restock the soil, and these species were able at least to maintain their position in spite of the later cultivation. At Woburn, after the initial samples were taken in January, no such opportunity offered during the first year of fallowing, and considerable reduction occurred, especially with *Capsella* and *Veronica buxbaumii*. The late ploughing had a reverse effect on *Alchemilla*, which is specifically an autumn-germinating species, with the result that far fewer seeds in proportion germinated at Woburn, and the reduction by fallowing was comparatively small. *Myosotis* is also largely an autumn-germinating species, heavily

8-2

reduced at Rothamsted and apparently unaffected at Woburn. No weight must be placed on the percentage increase on Woburn wheat, as the actual number of seeds was small enough to be seriously affected by the inevitable large experimental error. With all other species the response to fallowing was of the same order on the two areas, the variations being easily accounted for by the difference in the fallowing operations coupled with the probable variation in the rate of germination of any one species on the different soils under somewhat different climatic conditions.

(γ) *Recolonisation on Woburn soil during defective fallow.* An analysis of Table IX (given in Table X) shows that the weed species fall into three classes, according to their reaction to the conditions of the defective fallow from August, 1927 to July, 1928. The first of these classes in which the reduction was continued in the second year is quite distinct, but the other two overlap to some extent, as *Gnaphalium, Poa* and *Capsella* showed an increase on one soil but were not influenced by the fallowing on the other. In reality these two latter classes could be merged, as the fact that a species shows no reduction implies that some measure of recolonisation must have occurred to provide seeds to replace those eliminated by the fallowing operations. This would apply to *Vicia, Chenopodium* and *Veronica buxbaumii*, but the numbers of *Rumex acetosella* after fallowing were too small to consider seriously.

Table X. *Results of second year's fallow on Woburn soil compared with position after first year's fallow*[1].

Decrease	No significant effect	Increase
Myosotis	—	Veronica hederæfolia
Alchemilla	—	Arenaria
Papaver	—	Agrostis
Legousia	—	Juncus
Viola	Gnaphalium (on wheat)	Gnaphalium (on barley)
Veronica arvensis	—	Cerastium
Spergula	Poa (on wheat)	Poa (on barley)
Matricaria	Vicia	Stellaria
Lamium	Veronica buxbaumii	—
—	Capsella (on barley)	Capsella (on wheat)
—	Rumex acetosella	Senecio
—	Chenopodium	Polygonum aviculare

Without exception the species in the first column, showing continued decrease due to fallow, comprise those which germinate freely in the early autumn under favourable conditions, and which would therefore have sprung up rapidly after the August ploughing in 1927. The November cultivation cut these down, and the later plants which appeared during the following spring did not ripen sufficient seed to make good the autumn loss. In the case of *Myosotis, Alchemilla, Papaver* and *Veronica arvensis* some measure of recolonisation doubtless occurred, as the reduction by fallowing was less than under Rothamsted conditions. This was probably also the case with *Spergula,*

[1] For convenience, species are left in the order in which they occur in Table IX, instead of being arranged in alphabetical order.

Viola and *Lamium*, for which no comparative figures are available. *Legousia* and *Matricaria*, on the other hand, are late in flowering, and may have been cut down by the July cultivation before they had ripened seeds, since they were as greatly reduced as at Rothamsted.

The species showing *increase* after the second year's fallowing were types without any marked periodicity of germination, with the exception of *Veronica hederæfolia* and *Polygonum aviculare*. The proportion of seeds germinating in early autumn and eliminated by the November ploughing was much smaller than in the group considered above, and therefore a relatively heavy crop of weeds appeared the following spring. All the species would be seeding freely before the July cultivations, the supplies of fresh seeds being in excess of those destroyed by the November ploughing, causing an increase in the soil population. The tendency of seeds of *Polygonum aviculare* to germinate chiefly in the early months of the year brings it into this category, but it is very difficult to explain the increase in *Veronica hederæfolia*, as this is typically an autumn-germinating species, which would normally have been seriously depleted by the November cultivation. Since the numbers of this weed were quite small, little weight should be placed on this isolated discrepancy, which may be affected by experimental error, accentuated with scattered species.

(2) *Response of different species to identical methods of crop cultivation.*

When land is cropped the factors influencing the weed seed population are far more complex than when it is under fallow, as the demands of the crop and the type of season become of great importance, since they have a direct bearing on the question of deliberate human interference from the point of view of weed reduction. With autumn-sown wheat late ploughing is impossible, and large numbers of weed seeds which would be brought to the surface during a year of fallowing remain in a condition of dormancy, buried too deeply for germination. The fate of the seeds which do germinate depends upon many factors. From wheat drilling to the first spring harrowing a period of four or five months elapses, during which large numbers of seeds germinate, some of which produce seedling plants within that time. Others become so well established along the drills that nothing but hand-pulling will remove them, a process that is impracticable under modern field practice. Hand or "Planet" hoeing from April onwards reduces the number of plants between the drills, but it is the season which determines whether the weeds have already scattered seed, whether they are cut down before they are sufficiently developed to produce seed, or whether large numbers of fresh seedlings appear after hoeing and remain undisturbed to replenish the weed seed population before harvest time. The natural dormancy of a species is therefore of less immediate importance when land is cropped, as it is overweighted by the effect of other factors. It remains, however, a vital point with regard to future years, as it enables a species to have a reserve of viable seed even after a season so un-

favourable that fresh seed formation has been at a minimum. This affords one explanation of the apparent reappearance of a weed in quantity after it has been negligible for some time.

The natural result of the interaction of so many factors is that conditions which encourage some species and lead to a heavy increase in the seed population are adverse to others. As the conditions vary from year to year, the balance between the species alters, and in no two successive seasons can the weed population be expected to present a similar quantitative composition. If a species is abnormally abundant in any season, so that it stocks the soil heavily with its seeds, it is quite probable that it will be relatively abundant in the immediately succeeding years, though this does not necessarily always happen. The variation from year to year is rather difficult to follow from the actual number of weed seeds present on a given area, and can most easily be studied by comparing the relative numbers present during the experimental years for every hundred that were originally in the soil at the beginning

Table XI. *Number of viable buried seeds from equal areas in three successive years (Rothamsted). (All seven plots together.)*

Land cropped throughout 1925, 1926, 1927.

	Actual population 14 sq. ft.			Relative population in percentages		
	1925	1926	1927	1925	1926	1927
Sonchus arvensis	32	99	54	100	305	167
Myosotis arvensis	134	295	349	100	219	261
Matricaria inodora	18	40	20	100	218	109
Medicago lupulina	87	169	73	100	207	80
Veronica arvensis	942	1,909	1,204	100	202	127
Veronica buxbaumii	84	217	361	100	172	286
Galium tricorne	15	20	16	100	135	109
Alopecurus agrestis	4,792	6,329	6,562	100	133	137
Arenaria serpyllifolia	236	249	269	100	105	114
Papaver rhœas	46,183	40,227	39,078	100	87	85
Galium aparine	116	97	228	100	83	196
Alchemilla arvensis	3,632	2,850	2,720	100	79	75
Senecio vulgaris	266	196	96	100	73	36
Veronica hederæfolia	561	391	296	100	70	53
Anagallis arvensis	54	36	24	100	66	44
Stellaria media	103	63	29	100	61	28
Capsella bursa-pastoris	220	133	307	100	60	140
Polygonum convolvulus	49	26	9	100	53	18
Euphorbia exigua	165	84	21	100	51	13
Caucalis arvensis	75	39	80	100	51	107
Atriplex patula	374	168	124	100	45	34
Æthusa cynapium	127	43	36	100	34	19
Legousia hybrida	516	176	168	100	34	33
Polygonum aviculare	561	177	44	100	32	8
Bartsia odontites	130	36	20	100	27	16
Linaria minor	343	36	55	100	11	16
Scandix pecten	354	35	16	100	10	5
Total (excluding Papaver)	13,986	13,913	13,181	100	99	94

Table XI shows the actual number of viable seeds of the twenty-seven major species that germinated from all the samples, totalling 14 sq. ft. in area, taken from the cropped part of the plots during three successive experimental years. The number of poppy seeds always exceeded the aggregate of the rest of the species to such an extent that it has been necessary to consider them separately and to omit them in making comparisons between the other species.

Papaver showed the considerable decrease of 13 per cent. in 1926, but remained constant the next year. This first decrease may have been due to particular care being taken with the spring hoeing, with the deliberate intention of cutting down the poppy seedlings at the most vulnerable stage, since poppy was one of the chief weeds against which reduction measures were being directed. The total number of viable seeds of all other species was remarkably constant, showing hardly any change in 1926, and only being reduced to 94 per cent. of the original in 1927. Although the total number varied to such a small extent, very considerable fluctuations occurred for each species from year to year.

Calculation of the figures to a basis of every hundred present in 1925, representing the initial condition of the field, renders it possible to show the degree of increase or decrease in succeeding years for individual species. In the first season nine species showed increase, *Sonchus* being tripled, and *Myosotis*, *Matricaria*, *Medicago* and *Veronica arvensis* being doubled in quantity. The remaining seventeen species were reduced in varying degrees, *Linaria* and *Scandix* only persisting to the extent of about 10 per cent. of their original number.

In the 1927 season four of the leading weeds, *Sonchus*, *Matricaria*, *Medicago* and *Veronica arvensis* showed an average reduction of 50 per cent. and only two, *Myosotis* and *Veronica buxbaumii*, were significantly increased. On the other hand, among those weeds which were heavily reduced in 1926, *Galium aparine*, *Capsella* and *Caucalis* were more than doubled, while *Senecio*, *Euphorbia*, *Stellaria*, *Polygonum aviculare* and *P. convolvulus* were further reduced by more than one-half of their surviving number in 1926. These wide fluctuations are obviously correlated with the season, habit of growth of individual species, the time and thoroughness of cultivation, and the degree of crop competition, and studies on individual species would be necessary to ascertain with any accuracy the nature of this correlation. With an early season and late cultivation considerable increase might be expected in those species which germinate in autumn or very early spring, as they have time to mature many seeds before they are interfered with. On the contrary, a late season and early cultivation might allow the escape of those species which germinate most freely in spring, since more seedlings would come up after the hoeing and be able to recolonise the soil with seeds if they were able to withstand the competition of the crop. In an attempt to reduce annual weeds while the land is under crop, it seems probable that the greatest measure of success is associated with

two or more cultivations of which one is early and one fairly late in the season, as by this means a wide range of species is attacked at vulnerable periods. This is indicated in the present case. In 1926 harrowing began on March 17th, and hoeing on April 15th. This lapse of one month, without any later cultivation, was insufficient to bring about any significant reduction in the total number of buried seeds per unit area, although the numerical balance of species was altered. In 1927 cultivation was more thorough, with harrowing on March 22nd, horse hoeing April 21st, and hand hoeing May 5th. This third later cultivation was possibly the factor which aided in the reduction of the total weed seeds to 94 per cent. of the original supply.

(3) *Comparison of the effect of fallowing and crop cultivation on the seed population of the same species.*

The curves in Figs. 1–4 are derived from the relative populations given in Tables IV and XI. They represent the number of weed seeds, for every hundred originally present, that were found in the soil during 1926 and 1927 on fallowed and on cropped areas. To a certain extent the different species can be grouped according to their response to treatment, but care must be taken not to generalise too freely from the data given.

(a) *Species responding to cropping and fallowing in the same general direction.*

Euphorbia exigua (A) and *Polygonum aviculare* (B) were heavily and equally reduced by fallowing and cropping. Both species have a very limited period of germination, practically confined to the early months of the year. The spring cultivations were evidently favourably timed, and cut down these seedlings before flowering occurred, and there was no later germination from the remaining buried seeds. Restocking of the soil did not occur in either year and drastic reduction was the result.

Scandix pecten (C) was similarly affected, although its time of germination is in the autumn or very early in the year under field conditions. Its susceptibility to reduction under crop conditions is probably due to its late seed ripening, together with the lack of germination during the late spring and summer months. In 1926 the reduction appeared to be rather greater under crop than under fallow, but this difference might easily be due to experimental error, which is inevitably very large in an investigation of this nature.

Veronica hederafolia (D) resembled *Scandix* in its response, but was less adversely affected. The autumn and winter germination, coupled with the rapid flowering of the species, doubtless provided opportunity for early seed production with both forms of treatment, though the cultivations were sufficiently effective to prevent the main seeding and to cause a considerable steady reduction on balance.

With *Æthusa cynapium* (E), *Atriplex patula* (F) and *Polygonum convolvulus* (G) maximum germination occurs in the early months, but the period
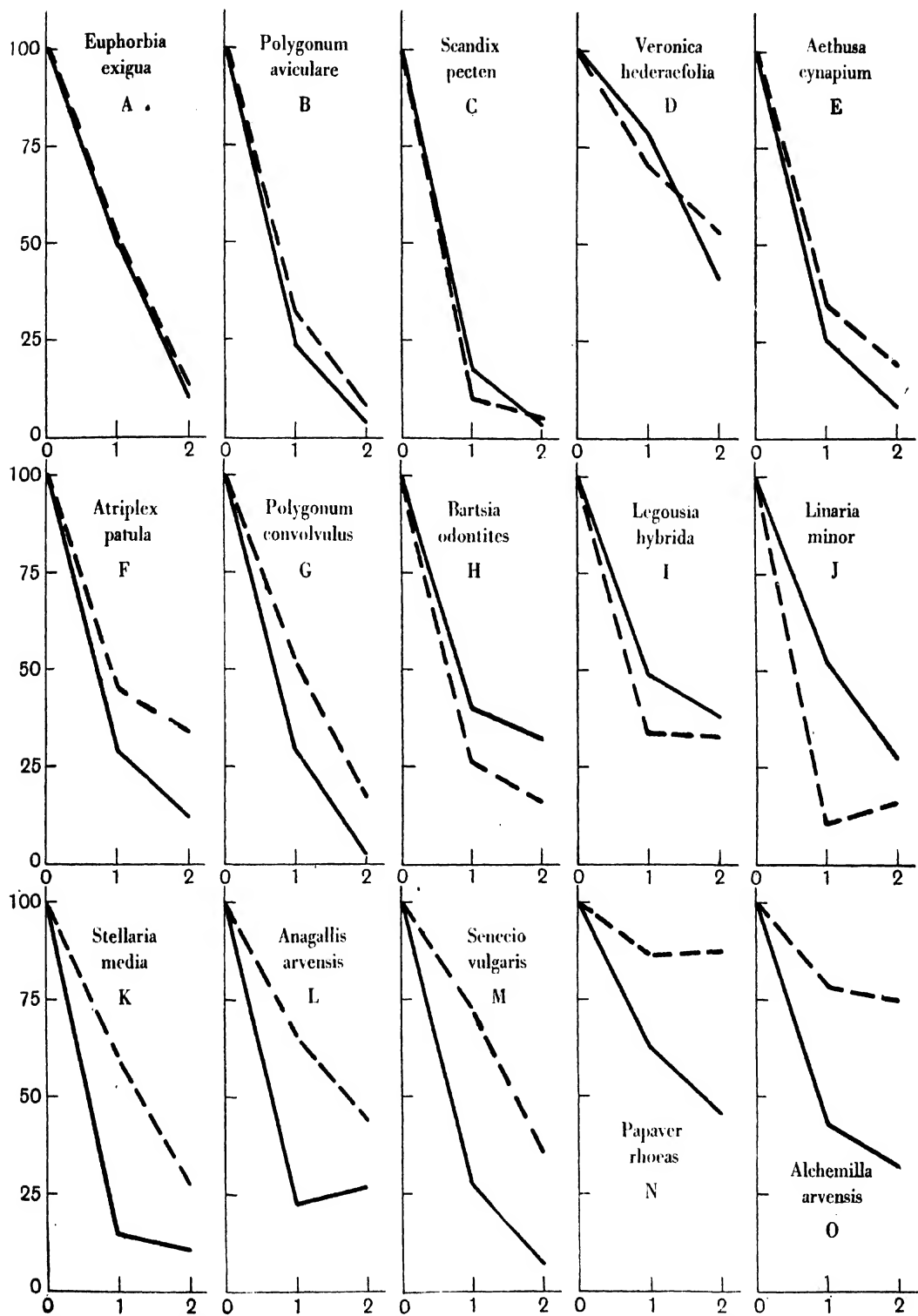
FIG. 1. Comparative effects of fallowing and cropping on the numbers of viable weed seeds in Rothamsted soil.

——— = Fallowed.   --- = Cropped.

0 = 1925, before experiment started.   1 = 1926, after 1 year's treatment.   2 = 1927, after 2 years' treatment.
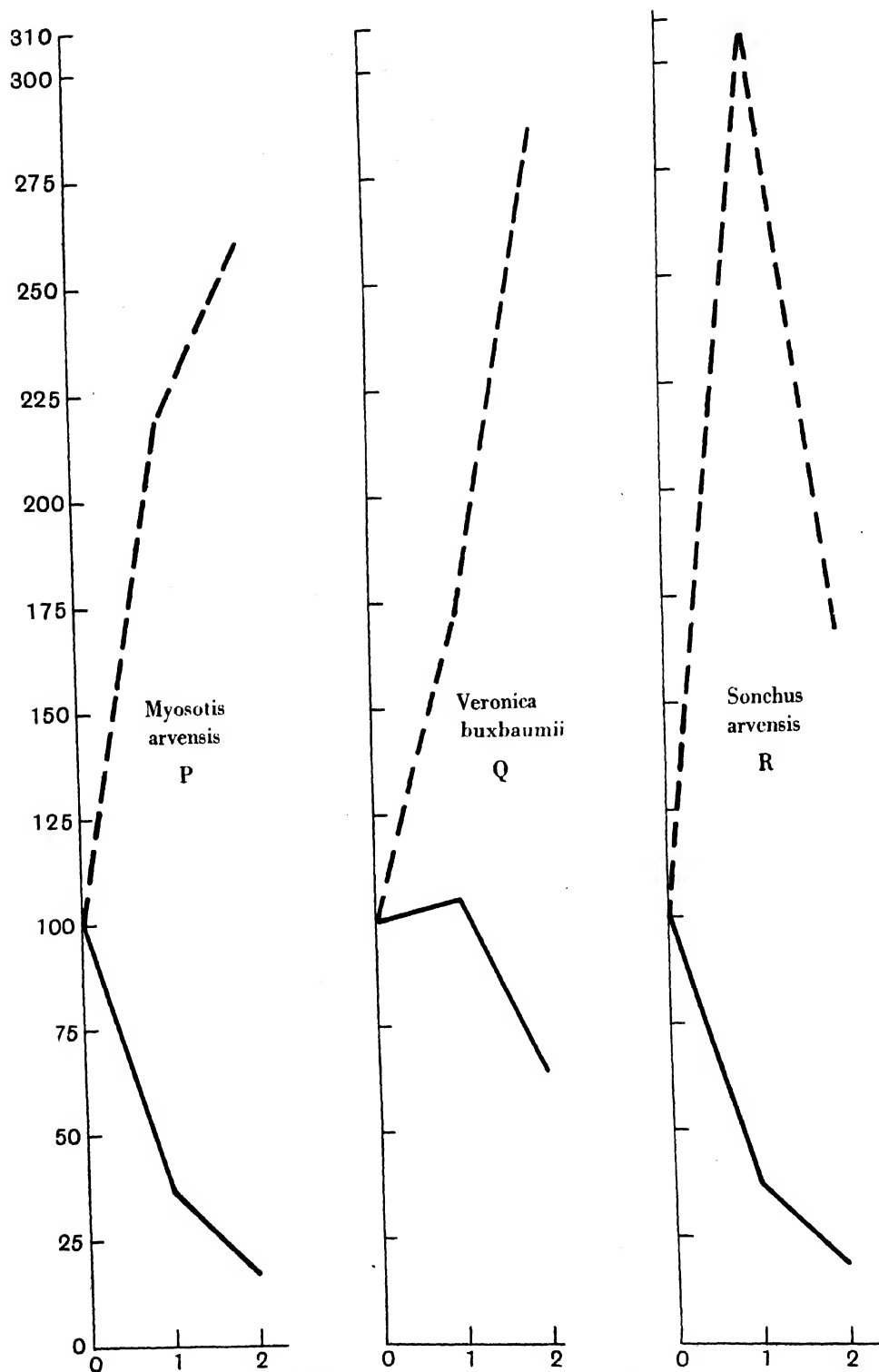
Fig. 2. Comparative effects of fallowing and cropping on the numbers of viable weed seeds in Rothamsted soil. ——— = Fallowed. - - - = Cropped. 0 = 1925, before experiment started. 1 = 1926, after 1 year's treatment. 2 = 1927, after 2 years' treatment.

is more spread over and seedlings appear to a later date. As a result, the reduction under crop was rather less than under fallow, as a certain number of the later seedlings escaped being cut down and replenished the soil population to some extent.
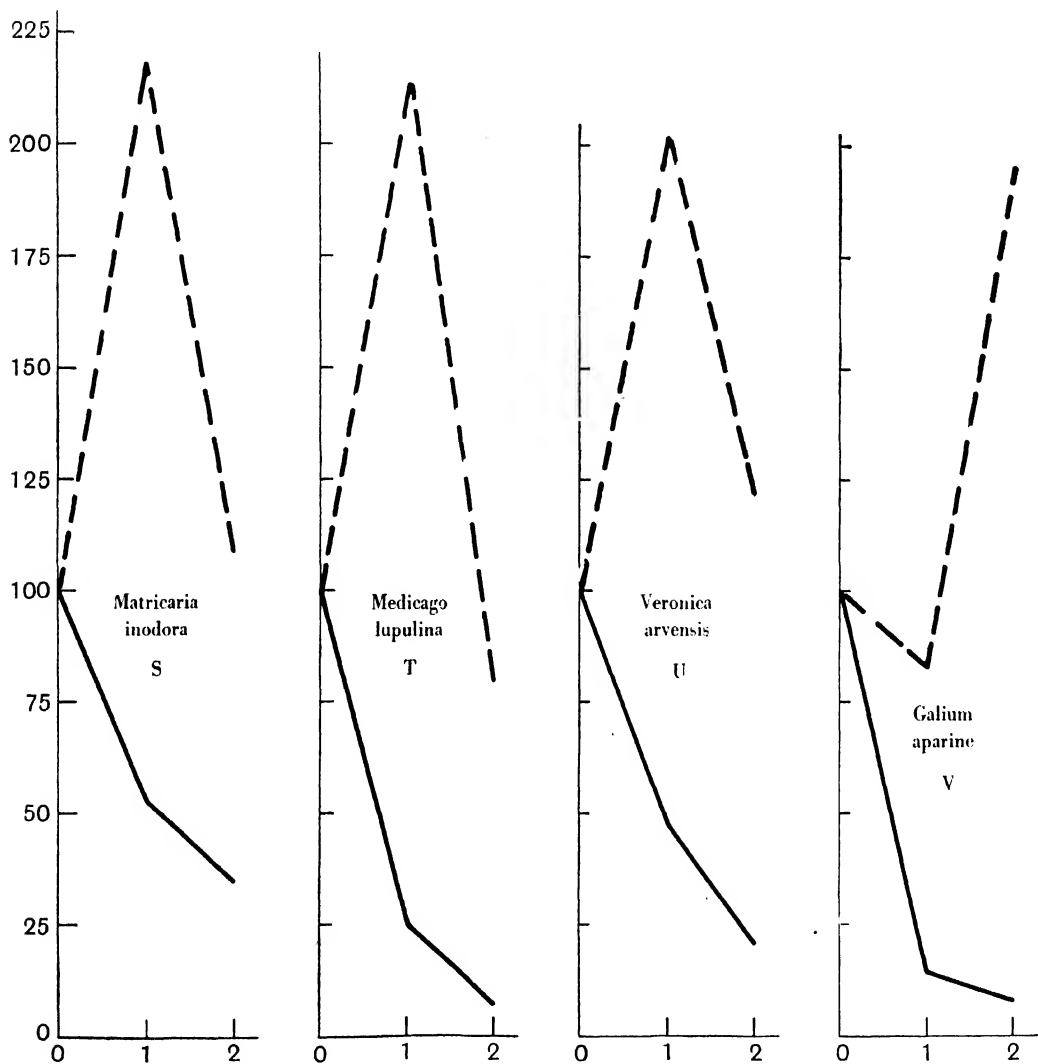
FIG. 3. Comparative effects of fallowing and cropping on the numbers of viable weed seeds in Rothamsted soil. —— = Fallowed. – – – = Cropped. 0 = 1925, before experiment started. 1 = 1926, after 1 year's treatment. 2 = 1927, after 2 years' treatment.

An unexpected reversal of the usual behaviour was obtained with *Bartsia odontites* (H), *Legousia hybrida* (I) and *Linaria minor* (J), in all of which the reduction under crop was greater than under fallow, particularly with *Linaria* in 1926. In all three cases the chief reduction under crop occurred in 1926, the

behaviour in 1927 varying with each species. It is difficult to account for this re-
sult unless it is in some way bound up with the different soil conditions induced
by fallowing and crop cultivation. The three species are noticeably irregular
in their occurrence in the field, and *Linaria* is very localised. As a general rule
they are more or less insignificant members of the weed flora, but occasionally
one or other forces itself into notice on account of its abundance in a particular
year. *Linaria*, too, is very susceptible to crop competition, and the number of
seeds that have germinated in these experiments gave promise of a much
heavier infestation than actually occurred, owing to the young plants being
crowded out by the crop. It must be remembered that the number of buried
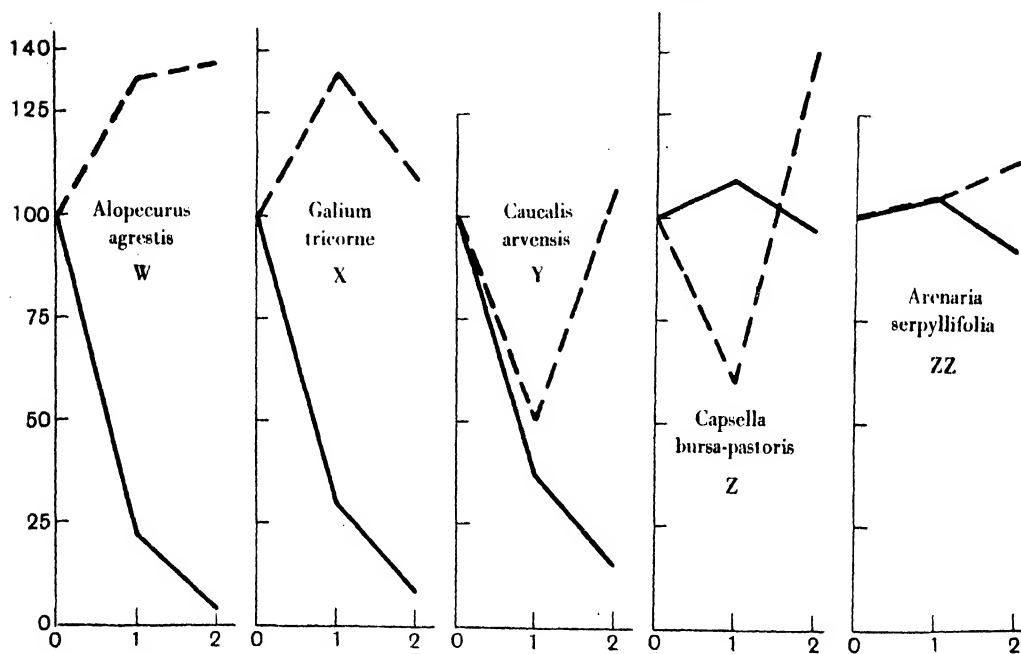
Fig. 4. Comparative effects of fallowing and cropping on the numbers of viable weed seeds in
Rothamsted soil. ——— = Fallowed. ———— = Cropped. 0 = 1925, before experiment started.
1 = 1926, after 1 year's treatment. 2 = 1927, after 2 years' treatment.

seeds per unit area at the time soil samples are taken is the result of the
effectiveness or otherwise of the previous season's crop or fallow, and has been
influenced by the climatic conditions during that season.

Stellaria media (K), *Anagallis arvensis* (L) and *Senecio vulgaris* (M) form
another group in which reduction of soil population occurred with both treat-
ments, fallowing being the more effective in the first year, and crop cultivation
more advantageous in the second. The three species begin to bloom early in
development and have a long continued flowering period, which enables young
plants to aid seed replenishment even though they may be cut down before they
have completed their growth. The behaviour of *Stellaria* and *Anagallis* in 1927
suggests that while the crop cultivation and competition continued to reduce

the buried seeds, there must have been periods during the fallowing when some seedlings were able to flower and fruit, thus keeping the soil population at much the same level at the end of the second season.

With *Papaver rhœas* (N) fallowing only reduced the buried seeds by about half, on account of their long period of dormancy, but crop cultivation had very little real effect, as a small reduction in 1926 was not continued the following year. This species is of different habit from any previously considered, in that it has a long period of growth before flowering occurs, and any plants which escape being cut down form such large numbers of seeds that relatively few are needed to replace the seeds which have been eliminated. This, coupled with the large proportion of seeds which escape by lying dormant, enables *Papaver* to maintain its position and to increase rapidly in favourable situations, rendering it a very pernicious weed on account of the difficulty in effecting a reduction. Fallowing is not an economic proposition, as recolonisation is very rapid from the dormant seeds, and so far no really effective method of eradication has been found. Fortunately, poppies are on the whole somewhat particular as to habitat, and it is only under unusual conditions, such as occur on Broadbalk with continuous wheat, that the weed will establish itself and spread freely on the less congenial soils. Doubtless, if this had been recognised twenty years ago, and the poppies carefully hand weeded from Broadbalk on their first appearance, the present state of affairs would never have arisen.

Alchemilla arvensis (O) closely followed *Papaver* in its behaviour, though the reduction was rather greater. Here again, the long period of dormancy kept an ample supply of seed in the soil, which gradually became capable of germination and provided means for re-stocking the soil later.

(b) Species responding irregularly to cropping and fallowing.

Most of the remaining species show much wider fluctuations than those so far considered, the effect of the two treatments being usually very different. With *Alopecurus agrestis* (W), *Myosotis arvensis* (P) and *Veronica buxbaumii* (Q) a steady increase in numbers occurred under crop in both seasons, while fallowing heavily reduced the first two and caused an ultimate reduction in the third. All have short dormant periods, and will germinate freely on coming into favourable positions, and if they are not cut they seed freely, whereas if they are killed out before seeding there are relatively few dormant seeds left to germinate later and make good the loss. Evidently the hoeing of the wheat did not catch these three species at a vulnerable time, and their seed population profited thereby. Although *Alopecurus* and *Myosotis* can be so effectively reduced by fallowing, no relaxation of effort is admissible, as the free and abundant seeding from the remaining small percentage in the soil very soon recolonises the cleared area unless stringent measures are taken directly the land is again cropped.

Sonchus arvensis (R), *Matricaria inodora* (S), *Medicago lupulina* (T) and *Veronica arvensis* (U) showed fluctuations in soil population under crop, though

all were heavily reduced by fallow. The period during which germination may occur is relatively longer, and in some conditions, as probably occurred in 1926, fresh seedlings must come up after the spring cultivations, and, given a favourable season, abundant seed formation takes place. In other cases, as in 1927, either little fresh germination occurred after cultivation or else the season was unfavourable or the crop competition so severe that the loss of buried seeds was greater than the replenishment. The same factor of prolonged germination gave fallowing its opportunity at successive cultivations, resulting in the heavy increase noticed. The result with *Matricaria* must be accepted with some reservation owing to the small number of seeds found in the areas sampled, though the bulking of the results from 140 samples, each consisting of three borings, tends to minimise the experimental error due to the irregular distribution of seeds over the area. The same applies to *Galium tricorne* (X), of which the numbers were really too small to give reliable information.

Galium aparine (V), on the other hand, was present in quantity, and in common with *Caucalis arvensis* (Y) was first reduced under crop and then showed a heavy increase the next season, whereas fallowing reduced both species effectively. *Caucalis* has a long period of dormancy and from field observations appears to be very dependent on season. *Galium aparine* has a medium period of dormancy, and no obvious explanation of the discrepancy in behaviour in succeeding years presents itself other than the interaction of season, time of cultivation and crop competition.

Capsella bursa-pastoris (Z) and *Arenaria serpyllifolia* (ZZ) resemble one another in their resistance to fallowing, discussed earlier (p. 115), but their response to crop cultivation was quite different. *Arenaria* showed a hardly significant increase in each year, the re-seeding being slightly higher than the reduction. Although *Capsella* more than held its own under the first year's fallow it was considerably reduced by crop cultivation in the first year, and was able to increase in the second season. It is hard to find a feasible explanation of this, unless the conditions under crop were such as to encourage an extra amount of germination after the cultivations had occurred, crop competition being then so heavy as to kill out the seedlings at a very early stage, preventing soil replenishment. It is quite possible that at the time of hoeing weather conditions were such that the crop gave protection and kept the soil in good condition as a seed bed, whereas on the fallowed area drying out may have occurred and more seeds remained dormant in the soil.

IV. Summary.

1. The weed seed population of the soil is greatly influenced by the type of crop grown. Soil conditions being similar, the composition of the flora under continuous wheat and barley is very much the same, but the relative abundance of the constituent species varies greatly, some being favoured by the wheat crop and others by the barley. On the whole, the spring cultivation

before barley sowing tends to keep the number of buried weed seeds below those occurring in the autumn ploughed wheat soil.

2. When fallowing operations are carried out the various species in the soil population are differently affected. Most species are reduced in number, but the degree of reduction ranges over a wide percentage, while a few species may even be increased. These variations seem to depend upon the correlation between the times of the fallowing operations and the periods of maximum germination of the different species, coupled with the length of their natural dormancy.

3. If the interval between processes of cultivations are too prolonged some species are able to reach maturity and replenish the soil with so many seeds that the beneficial effect of the fallowing is entirely lost. Weed species vary considerably in their ability to recolonise the soil in this way.

4. When land is cropped the processes of cultivation affect the weed flora more variably than is the case with fallowing. On the same area some species may be drastically reduced while others may be doubled or trebled in quantity. This again depends on the correlation between the date of sowing the crop, the method of cultivation, and the habits of the weed species as regards maximum period of germination and length of natural dormancy.

5. Some weed species respond to cropping and fallowing in the same general direction, being reduced by both methods of cultivation. Other species may be generally reduced by fallowing, but behave variably under crop, being increased or decreased in different seasons.

6. From the agricultural point of view it is apparent that unless fallowing operations can be carried out with a much greater degree of thoroughness than is usual, reduction of many weeds can be effected almost as well and more economically by intensified cultivation while the land is under crop. Other species, however, which tend to increase in some seasons under crop conditions, may be more effectively dealt with by fallowing if their predominance justifies the expense, which implies loss of crop as well as the cost of numerous cultivations.

A COMPARATIVE STUDY OF THE ALGA FLORA OF TWO SALT MARSHES. PART II

By NELLIE CARTER[1].

(With twenty-six Figures in the Text.)

CONTENTS.

IX. SYSTEMATIC LIST OF THE SPECIES OBSERVED[2].

ISOKONTAE.

SEVENTEEN species of this group were recognised, of which about seven only are common to both marshes. Quite possibly certain other species are also common to both, as for example *Vaucheria*, which is not often found in fruit, and is therefore not often specifically identifiable.

Ulothrix flacca and *Enteromorpha minima* are important forms occurring at Canvey although absent from Ynyslas. Both are abundant in the moister marginal zones, *Ulothrix* especially in late winter and spring. *Enteromorpha minima* is a characteristic epiphyte on all marginal plants and débris. The only form of any importance at Ynyslas which does not occur at Canvey is *E. compressa*, which although not abundant, is frequently present as an epiphyte on marginal escarpments. *E. percursa*, which is so abundant at Ynyslas does not in general occur at Canvey. There is one solitary record for it at Canvey, a fact which it seems rather necessary to verify. On the whole, the Chlorophyceae seem to be more important at Ynyslas than at Canvey, since here they may be found in quantity among the grasses all the year round, whilst in the latter locality they become abundant in the marginal zones chiefly in spring and summer.

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[1] From the Botanical Department, East London College.

[2] The order of the genera adopted is as far as possible that found in **West** and **Fritsch**. The letters A, B, etc., refer to the phanerogam zones of the salt marshes (cf. **Carter** (**9**), pp. 347–360) and the numerals I, II, etc., refer to the months of the year in which the alga has been found.

There is practically no zonation amongst the Chlorophyceae themselves with the exception of *Ulothrix* spp. which, in general, are confined chiefly to the lower zones.

ULOTRICHACEAE.

1. **Ulothrix flacca** (Dillw.) Thur., Wille, 1901, p. 18, t. 1, f. 54–57, t. 2, f. 58–63.

Canvey. A, B, C, and D. x–vi. Fig. 1, *1–6*.

This alga, which grew very luxuriantly at certain times of the year, agreed very well with the description given by Wille (**51**). The filaments were very long, and about 30–50µ in diameter. The cell wall is of some thickness and shows distinct lamellae around each cell. In addition there seems to be a firmer sheath to the filaments which is much more resistant than the lamellated part of the wall. This outer sheath does not seem to be jointed or interrupted at the cross walls, of which it is quite independent. The inner lamellated strata are capable of swelling considerably as they seem to do at times of zoospore formation. Not infrequently the outer "cuticle," if one may so term it, seems to fail to grow as rapidly as the living cell, resulting in the appearance shown in Fig. 1, *4*. As described by Wille, the filaments are frequently divided into sections separated by thicker cross walls, the sections appearing to result from the repeated division of a single original cell.

The cells each possessed a girdle-like chloroplast, usually of fairly massive proportions, containing 4–6 pyrenoids and completely encircling the cell. In cells actively growing and therefore possessing a somewhat scanty chloroplast, the nucleus could be seen even in the living cells, often occupying a parietal position in a perforation of the chloroplast. In cells with more abundant content the nucleus is masked by the chloroplast which lies outside it.

Hazen (**27**) says that the vegetative cells possess one pyrenoid, but that in cells which are reproducing there may be more. Cells possessing a single pyrenoid were exceptional in the Canvey material, four being quite the usual number. Possibly this may be correlated with the larger size of the cells, which were 30–50µ in diameter as contrasted with 10–25µ, the limits given by Collins (**11**) and Hazen (**27**).

The alga is an extremely important one on the Canvey marsh in the early spring. Isolated filaments may be found during October–January, but by February it increases in bulk amazingly, and during February and March it is the most important alga on the marsh, being especially abundant in the marginal zones (see also Parts I and III). Cotton (**14**) also recorded this alga in February in Clew Bay and Achill Island, as thin, felt-like masses. At Canvey it is most important as far up as the *Aster-Salicornia* zone; it does not flourish much above that level, although it may be found in the *Obione* and *Aster-Glyceria* zones, and in the marginal parts of the latter it may be quite abundant. After March it rapidly decreases in quantity and is only present in

small amount until June, after which it was not observed at all until about
November or December.

Zoospores were formed abundantly during the maximum growth of the
alga. Each cell produced a large number, which are usually extruded into a
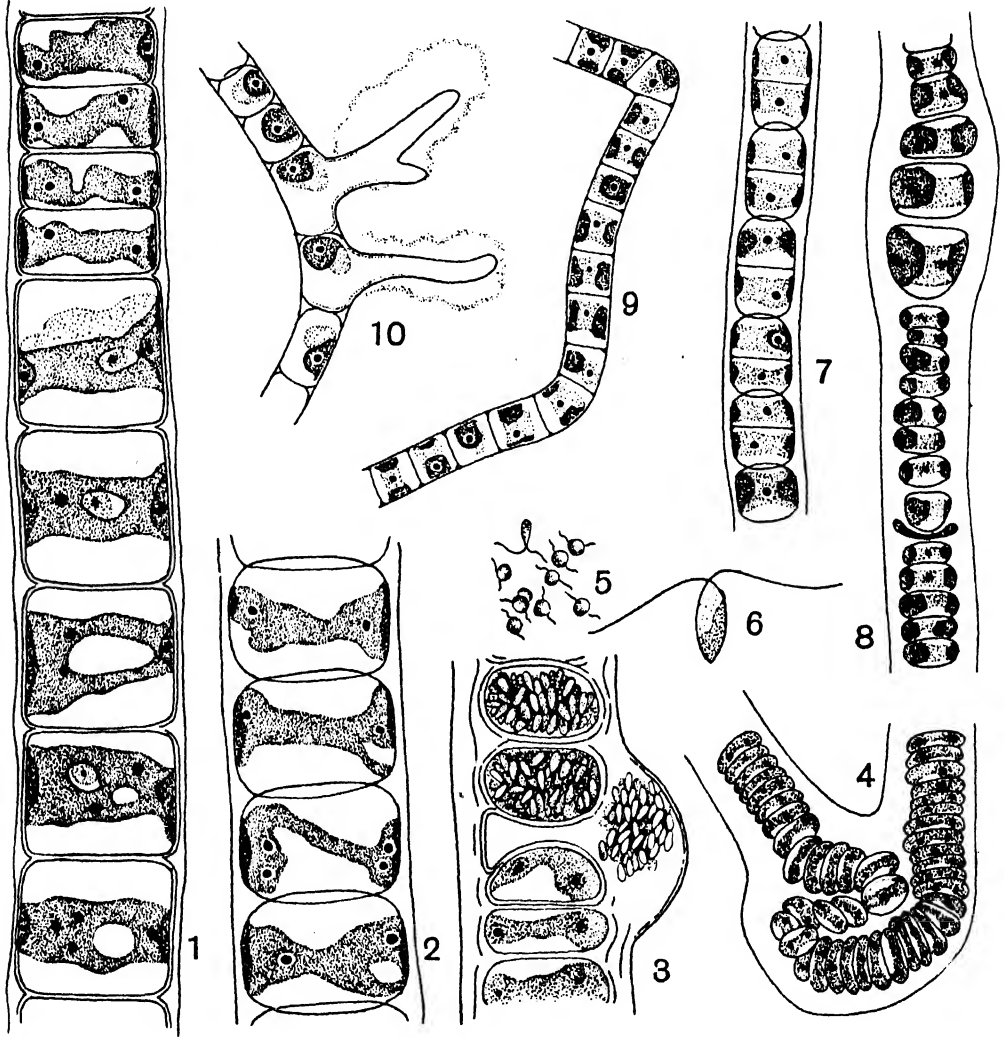
Fig. 1, *1–6.* *Ulothrix flacca* (Dillw.) Thur. *1, 2,* vegetative filaments; *3,* forming swarmers;
4, showing a frequent abnormality; *5, 6,* zoogonidia. *7, 8, U. pseudoflacca* Wille; *9, 10, U. sub-
flaccida* Wille. *1, 2, 3, 5, 7, 8, 9* and *10,* × 545; *4,* × 218; *6,* × 1910.

vesicle before being released. Occasionally they are imprisoned by the outer
"cuticle," which fails to release them (Fig. 1, 3). The zoogonidia were not ob-
served to conjugate, yet they agreed entirely with the description given by
Wille (**51**, p. 21) for the gametes of the alga. They were spindle-shaped at first,
later becoming nearly spherical, and possessed a stigma, two cilia and a parietal
chloroplast. A pyrenoid could not be demonstrated.

2. **U. pseudoflacca** Wille, 1901, p. 22, t. 2, f. 64–81.

Canvey. A, B, and D. ɪɪ–ᴠ.
Ynyslas. B, C, and D. ɪ–ᴠ.   Fig. 1, 7, 8.

The filaments were $12-21\mu$ in diameter, and the cells usually very short, being sometimes only one-fifth as long as broad, but rarely slightly longer than broad. The cell wall showed essentially the same features as *U. flacca*, but there are very distinct differences in the cell structure. The form identified as *U. pseudoflacca* Wille has its chloroplast in the form of an incomplete band and usually possesses a single pyrenoid until the time of cell division. *U. flacca* has a number of pyrenoids, and its chloroplast forms a complete girdle. Wille (**51**) in his description does not make these points clear, and it is possible that he did not realise the true facts. Both Collins (**11**) and Hazen (**27**) are disinclined to recognise *U. pseudoflacca* as a species distinct from *U. flacca*, but in the opinion of the writer, because of its smaller size, its different chloroplast and solitary pyrenoid, it is a distinct form. Moreover it occurred both at Canvey and at Ynyslas, whilst *U. flacca* has not been seen on the Welsh marsh, and therefore seems to have more specialised requirements as regards substratum. In both localities *U. pseudoflacca* was restricted to the lower zones, and is a strictly vernal species, not appearing except very rarely until February or March, and becoming sparse again by April or May. It never reached the same abundance as *U. flacca*, occurring only as occasional threads among other algae, at Canvey often with *U. flacca*.

3. **U. subflaccida** Wille, 1901, p. 27, t. 3, f. 90–100 (? *U. implexa* Kütz. in Hazen, 1902, p. 153, t. 21, f. 1 and 2).

Canvey. A, B, and D. xɪ–ɪᴠ.
Ynyslas. B, and C. xɪ–ᴠɪ.   Fig. 1, 9, 10.

There seems to be some doubt as to the correct name of this species. Hazen (**27**) and Collins (**11**) have adopted the name *implexa*, but Wille (**51**, p. 22) has pointed out that Kützing had not intended to give this name to a marine species, and in consequence he re-described several marine forms of the genus. The alga found in this investigation agreed fairly well with Wille's description of *U. subflaccida*. The filaments were $6-10\mu$ in diameter, and the cells slightly less than, or up to twice as long as their breadth. The cell wall was much thinner than in the two preceding species, and of simpler construction, appearing to lack the "cuticle" of the stouter species. Each cell had a plate-like chloroplast appressed to the wall, containing a single pyrenoid, and as described by Wille, very often there was a considerable part of the wall free from chloroplast. The alga occurred sparsely amongst other algae, and was never found in great quantity. Both Wille and Hazen state that it usually occurs covered with water, but in the present case, although inhabiting the marginal zones of both marshes, it must be exposed to the air for many days at a time. Reproductive stages were not observed. Like the preceding species, *U. subflaccida* is a strictly vernal form. On rare occasions, the alga was

observed to form short rhizoids, especially when growing on the shifting sand at the margin of the Ynyslas marsh (Fig. 1, *10*).

<center>CHAETOPHORACEAE.</center>

4. ? **Endoderma perforans** Huber, 1893, p. 316, t. 14.

Canvey. Rare on soil, *Obione*, escarpment to *Glyceria* zone.
Ynyslas. On *Rivularia* colonies and on soil of escarpments. VI–IX. Fig. 2.

This peculiar alga seemed to be equally capable of establishing itself on the firm mud of the marginal escarpments at Ynyslas or on the colonies of *Rivularia*, which often encrust such escarpments or other parts of the marsh. Huber described *Endoderma perforans* from dead leaves of *Zostera*, where it was penetrating the epidermis and ramifying in the tissues. In the present case the alga was living on and within the small hard colonies of *Rivularia*, sending its filaments deep into the gelatinous colonies between the threads of the blue-green alga (Fig. 2, *1*). The form living on the soil was associated with *Phormidium* between the *Rivularia* colonies, but it is a little uncertain whether this alga is identical with the one inhabiting the *Rivularia* colonies. It was very difficult to separate the soil form from soil particles, but the general habit of growth, so far as could be seen, was very much the same as in the endophyte of *Rivularia*. Sometimes, however, the cells of the filaments were very long, forming long slender threads, which, being sparsely branched and having feeble plastid content, were very suggestive of fungal hyphae (Fig. 2, *3*).

In the case of the *Rivularia* colonies, it was difficult to obtain a good idea of the endophyte and its method of branching, because it was necessary to crush the *Rivularia*, often with the result that the *Endoderma* threads broke up. It appeared, however, that sometimes the green filaments of the endophyte spread out in a radial fashion from the centre of the colony towards the periphery, the cells tending to swell slightly when reaching the outer margin of the colony and also to branch more profusely. Again, sometimes the ends of the threads, having reached the periphery of the colony, proliferate to form a complex group of cells, from which filaments are given off, creeping along the surface of the colony like runners (Fig. 2, *1a*, *2*). The proportions of the cells varied very much, the cells being usually nearly as broad as long, 8–14μ wide, 14–20μ long, but sometimes very long and slender, 3–5μ wide, 14–70μ long. Although the short broad cells were to be found chiefly at the ends of the branches, several changes of diameter in the same filament were not infrequent. The cells usually possessed a parietal chloroplast in which one or sometimes two pyrenoids were embedded. Some of the short cells often had more pyrenoids, and frequently showed dense contents, which may indicate that they were about to form reproductive bodies, though none of these were seen.

FIG. 2. *Endoderma perforans* Huber. *1*, filaments inhabiting colony of *Rivularia*, ×196; *2, a* in *1*; *2–4*, ×490.

ULVACEAE.

Minute fragments of *Monostroma* sp. were occasionally found as epiphytes on the persistent dead stems of *Aster tripolium* at Canvey in the early spring, but not in sufficient quantity for determination.

5. Enteromorpha minima Nägeli in Collins, 1909, p. 201.

Canvey. A, B, C, and D. All the year round.   Fig. 6, *1–3*.

Examples of this alga could usually be found as epiphytes on *Salicornia*, *Aster* or *Obione*, or occasionally amongst other algae on the ground. It varies very much in the size of its fronds, which are sometimes microscopic and sometimes reach a length of several centimetres. Sometimes it is deposited as drift on the lower parts of the marsh, still attached to fragments of the peripheral parts of phanerogams.

6. E. percursa Ag. in Collins, 1909, p. 197.

? Canvey. B. 1927. XI.
Ynyslas. B, C, D, and F. All the year round.

This alga formed one of the most important constituents of the Ynyslas marsh, although it was probably less general than *Rhizoclonium*. It prefers the intermediate zones, viz. Armerietum and Lower Festucetum, where it often forms local mats 5–8 cm. in diameter and as much as 2–5 mm. in thickness. The soft mass readily splits into thin sheets, and the lower strata, although still alive, are not as healthy as the top ones. At the margins of the marsh, in the Glycerietum, it is always rare, probably owing to disturbance due to tides, but locally parts of the escarpments may be clothed with it. Only very rarely is it found in the Juncetum and never in the Upper Festucetum. It is peculiar that it was only found on one occasion at Canvey, when it was quite abundant locally in the *Aster-Salicornia* zone. Unless it is subsequently found there again this record must be left in abeyance for confirmation.

7. E. compressa Grev. in Collins, 1909, p. 201.

Ynyslas. Marginal escarpments. All the year round.

The plants varied in size from a few millimetres to several centimetres in length, and sometimes reached 1 cm. in diameter. They were always attached by a definite holdfast, sometimes to the exposed roots of phanerogams or to grains of sand on the vertical eroded escarpments of the marsh, or to larger algae. The fronds were tubular at the base, becoming broader higher up where they were usually compressed to form a ribbon-like thallus, though at times they were alternately inflated and flattened.

8. Enteromorpha prolifera J. G. Ag. formae.

Canvey. A, B, C, D, and E. All the year round.
Ynyslas. A, B, C, D, and F. All the year round.   Figs. 3, 4 and 5.

Apart from the species of this genus identified above, examples of *Enteromorpha* in very varied morphological form were very common on both marshes.

The different forms varied from long slender filaments, simple or richly branched, and found chiefly in the marginal zones, to peculiar convoluted prostrate masses lying anchored on the soil between the grasses of the *Glyceria* zones at Canvey or amongst the *Juncus* haulms at Ynyslas. Although differing so widely in morphological form it is believed that all these are modifications of the same species. Growths of *Enteromorpha* are much more conspicuous at Canvey than at Ynyslas. In the first locality the alga is most abundant from May to July, although it may be present in smaller quantity at other times of the year. On the Welsh marsh it did not show the same conspicuous seasonal periodicity, but this may only be due to the fact that it does not play such an important part in the flora of that marsh. At Ynyslas it is only very rarely an important constituent of the turf zones; on the other hand it is usually quite abundant on the marginal mud flats, or festooning the marginal escarpments.

It seems likely that two distinct forms are concerned, which will be described as A and B.

A. The first one usually has simple slender filaments without true branches. The threads are often many inches in length; they seem to have no polarity and lie prostrate on the ground forming merely a thin weft or a thicker carpet. An attaching holdfast has never been observed, and the filaments are practically the same width throughout their length. The most slender filaments are only about 40μ in diameter, but the stouter ones may reach a diameter of 600μ.

The cells, which are fairly large and almost rectangular, are arranged, as a rule, conspicuously in longitudinal rows, except for local disturbances, and the rows are sometimes twisted in a slight spiral round the tubes. The chloroplast does not entirely fill the cell, and there are usually two or three pyrenoids (Fig. 3, *1, 4*).

Filaments less than 100μ in diameter are as a rule quite simple and destitute of lateral outgrowths, but wider threads are sometimes invested with what may be termed proliferations. These are slender outgrowths of uniform width, sometimes only one cell in diameter, sometimes of greater width and possibly bearing other proliferations (Fig. 3, *2, 3*). These proliferations are of practically the same diameter throughout their length, and true branches, showing a difference in width at the base and apex, are almost never seen.

In filaments of about 500μ or more in diameter the longitudinal arrangement of the cells may be locally interfered with, and in such spots the cells tend to be polygonal rather than rectangular. Such disturbances are probably due to two causes, resulting either from the formation of proliferations, or from the irregular inflation of the larger tubes, which tend to collapse and bulge at intervals. It is obvious in Fig. 3, *3* and *4* that the longitudinal arrangement of the cells is lost when proliferations begin to develop, and also that the contents of neighbouring cells tend to concentrate towards the point where the
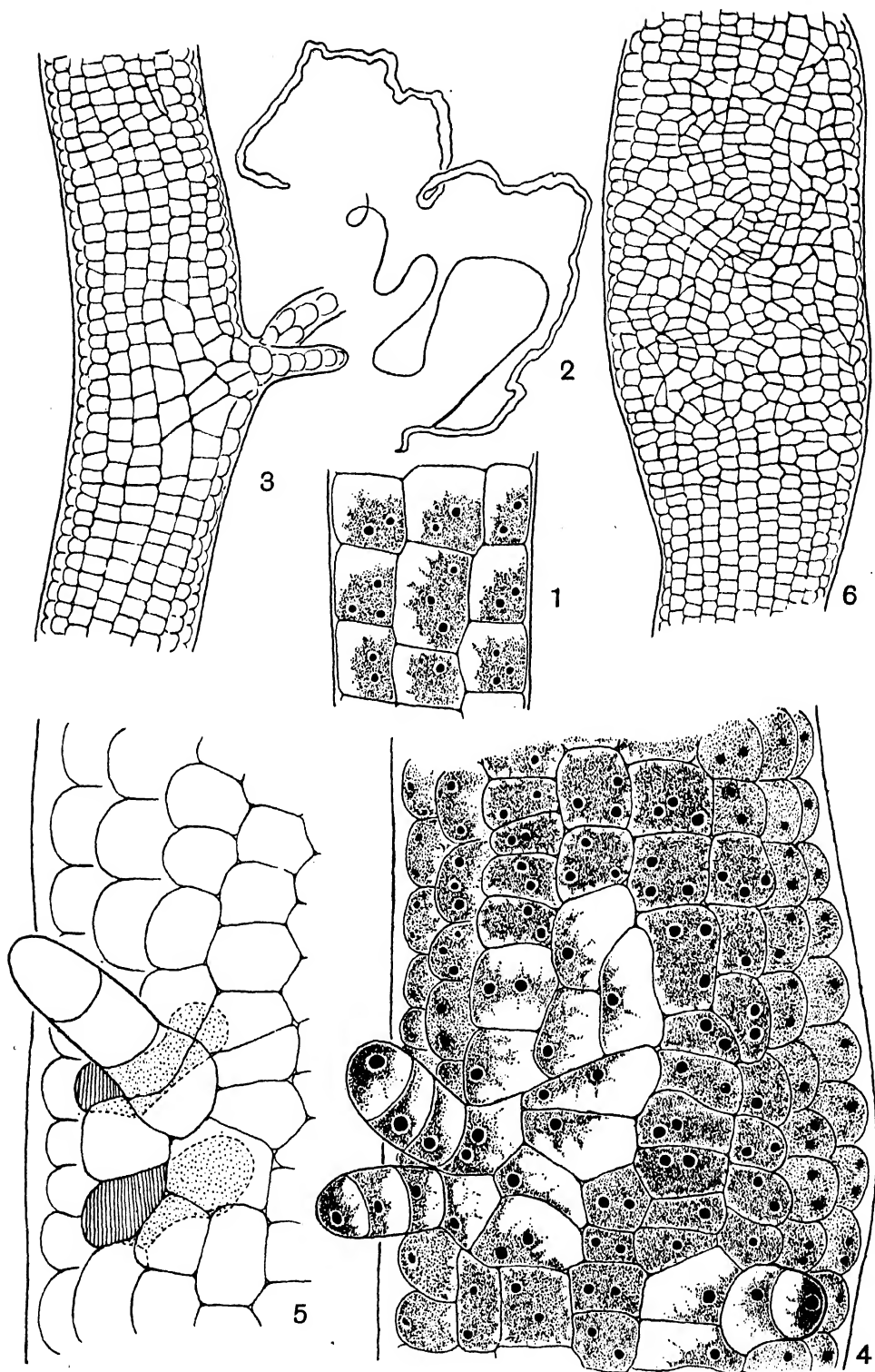
FIG. 3. *Enteromorpha ? prolifera* J. G. Ag. var. *tubulosa* Kütz. *1, 4* and *5*, × 613; *2*, × 2; *3* and *6*, × 245.

outgrowths are being formed. Fig. 3, *5* shows a peculiar case in which two cells have formed internal outgrowths projecting into the cavity of the tube.

The bulging or irregular inflation of the fronds may possibly be a result of the subaerial habitat of the alga. The filaments lie on the mud and are flooded at rare intervals by muddy tidal water, which deposits a layer of silt over them. Thus the threads get more or less firmly fixed down to the substratum by the deposited silt. This means that as growth of the thallus proceeds the elongation and expansion of the cells is rendered difficult in certain spots where the tube is adhering to the substratum. If the thallus is fixed to the soil at two separate points, it will in these circumstances expand laterally as a bulge between the two points, and in the bulge the dividing cells will push their way in any direction possible, so that the longitudinal arrangement is quite lost (Fig. 3, *6*).

It seems likely that the more slender filaments of this form may have their origin in the stouter fronds, some of which bear very long proliferations which may get broken off and become independent (Fig. 3, *2*).

This form of *Enteromorpha* is characteristic of certain parts of the Canvey marsh, especially the escarpment from the *Aster* zone to lower levels, and extends as far up as the *Obione* and the *Aster-Glyceria* zone. Thus it seems to require the moister parts of the marsh, but it does not extend down into the channels much further than 3 ft. beneath the *Aster* level. It has never been observed in the *Glyceria* zone at Canvey and it seems doubtful whether it occurs at all at Ynyslas. Attempts were made at Canvey to transplant sods bearing this alga from the *Aster* zone into the *Glyceria* zone. In all cases the surface of the transplanted soil became bare in a few months, indicating that the conditions in this zone are not suited to its growth. For this reason it seems likely that form A is distinct from form B, which flourishes even in the *Glyceria* zone. It is very difficult to name estuarine forms of *Enteromorpha*, but possibly A may be ascribed to *E. prolifera* J. G. Ag. var. *tubulosa* Kütz.

B. This form of *Enteromorpha* is much more variable than the last and often reaches a much greater size. It may at times possess a basal holdfast, and is branched, sometimes having branches of more than one order. In addition it may bear numerous slender proliferations. The cells are more angular than in A, and rather smaller, with denser contents and usually one pyrenoid. In the younger parts of the thallus the cells are in longitudinal rows (Fig. 5, *4*), but in the older parts, this arrangement is lost (Fig. 5, *5*). It has a much wider distribution on the marsh than the first form, though its morphology varies tremendously in the different habitats (cf. Figs. 4 and 5). At Canvey it occurs in all zones from the marginal mud to the *Glyceria* zone and it has also been found in the *Armeria* zone near Pantile Farm (see Carter (**9**), p. 359). At Ynyslas it was likewise found everywhere from the open mud flats to the Armerietum, and also in the Juncetum zone. In the Lower Festucetum it is only represented by small fragments. It forms at Ynyslas the greatest bulk of the unattached

weed which lies free on the mud flats or is anchored on the *Salicornia* plants. In less quantity it occurs also in the ropes of alga lying in the Glycerietum (see Carter (9), p. 349). At Canvey it is subsidiary to the first form A on the *Aster-Salicornia* escarpment, but in all other zones it is of far greater importance. The determination of this form, like A, presented great difficulties and its identity can only be suggested tentatively. It seems to belong to *Enteromorpha prolifera* J. G. Ag., but is present in four different morphological forms, which will now be described.

I. The simplest is an attached form, though it is more often found lying free, torn away from its substratum. It shows a holdfast at one end, and is attenuated at both extremities, consisting merely of a simple unbranched frond, up to $1\frac{1}{2}$ mm. in diameter at the widest part, and as much as 5 cm. long (Fig. 4, *1*). It may bear a few proliferations, especially in the region of the holdfast (Fig. 4, *2, 3*). The larger plants may be irregularly inflated and crinkled. This type is not abundant, but it has been found amongst the *Enteromorpha* tangles in the *Aster-Glyceria* zone at Canvey, and also in the masses of alga in the Salicornietum at Ynyslas. Fig. 4, *5* is an unusual plant, which has a proliferating flat thallus of some breadth, and also numerous short slender proliferations.

II. More often the plants are detached and show merely torn extremities, though they are still healthy. The fronds are usually slender and much branched, the stouter parts not greatly exceeding 2 mm. in diameter (Fig. 4, *4*, Fig. 5, *1*). This type is frequent in the marginal masses of alga lying on the shore at Ynyslas, of which it forms the bulk, and it also occurs as far up as the Armerietum, though in less quantity and in more fragmentary condition. At Canvey it is sparse with type I in the *Aster-Salicornia* zone, extending into the *Obione* and *Aster-Glyceria* zones above, and into the bare channel for a short distance below.

III. A more conspicuous form of *Enteromorpha* takes the form of long tubes, varying in diameter from 1 to 10 mm. and reaching as much as 30 cm. in length, irregularly bulging and contracted at intervals, sometimes bearing numerous proliferations (Fig. 4, *6*), sometimes appearing to be quite free from them. This form is frequent at certain times of the year, lying on the mud flats at Canvey and Ynyslas, especially in July and August. The plants are quite unattached and at the mercy of the tides. Thus they must very often be buried or washed away. This may account for the fact that at Ynyslas in July, 1929 and 1930, the mud flats were quite destitute of *Enteromorpha*, whilst in July and August, 1928, these wide tubular fronds had been very abundant.

If these plants are buried in the sand they readily proliferate new fronds. When collected, the basal horizontal tube of the plant shown in Fig. 5, *3*, was lying buried in the mud of the Salicornietum at Ynyslas. The cells composing this subterranean part were already dead or dying, but abundant new fronds had been developed which were streaming out above the surface of the sand. Some of the new filaments were quite simple and unbranched, or with short
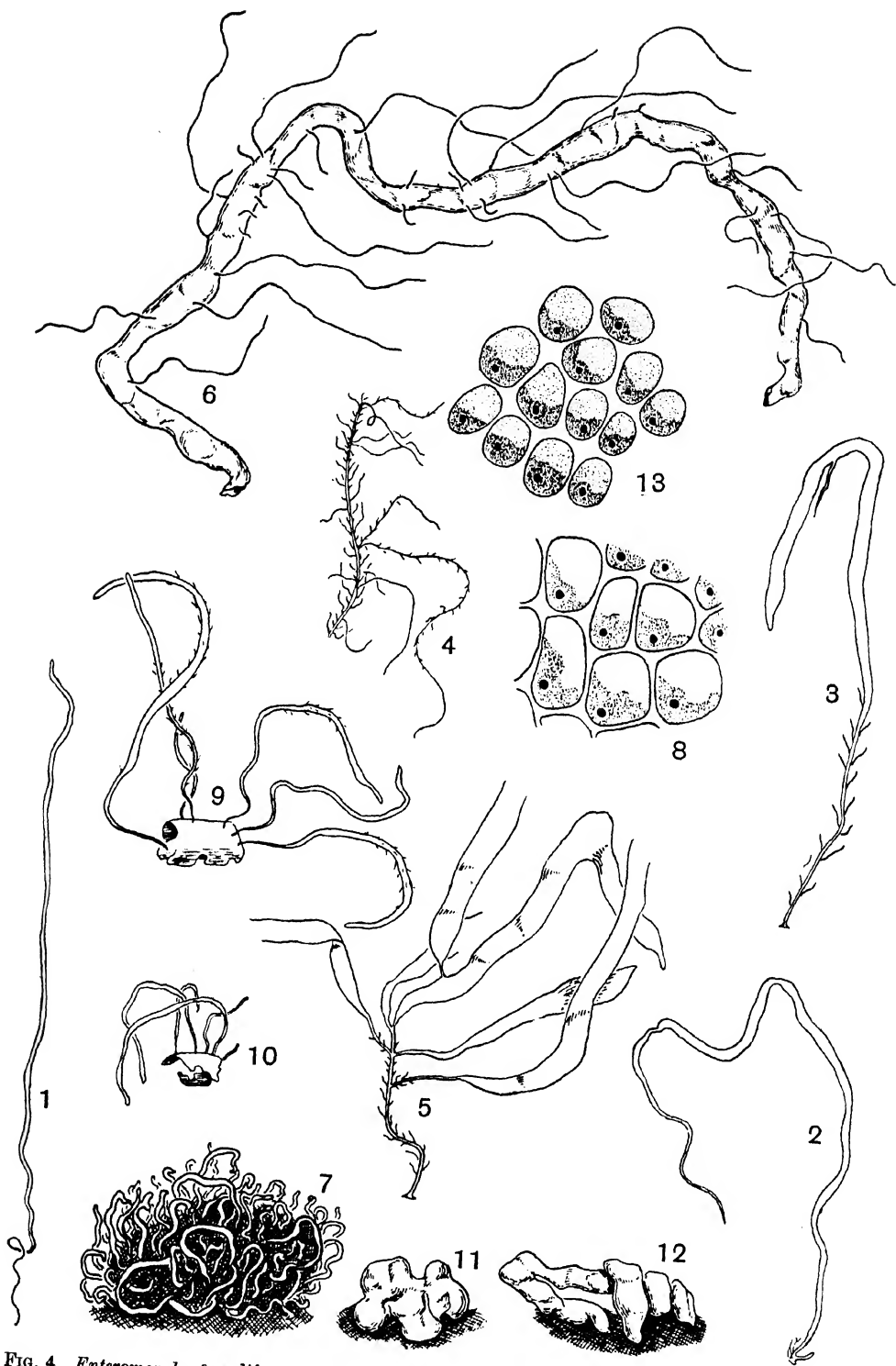
FIG. 4. *Enteromorpha ? prolifera* J. G. Ag. *1–7*, different examples; *8*, portion of thallus from *7*; *9, 10*, individual plants from *7*; *11, 12*, other examples; *13*, part of thallus of *11*. *1, 2, 11* and *12*, ×2; *3* and *5*, ×4; *4, 6, 7* and *10*, ×1; *8* and *13*, ×613; *9*, ×3.

proliferations, but others were abundantly branched. Many such plants were found anchored in the mud by means of the fragments of the old wide tubes at Ynyslas in June, 1928. It is not known whether the old tubes which had proliferated belonged to the season 1927 or 1928, but the probability is that they were of the season 1927, since no wide tubular forms were observed here in 1928 until July. Possibly, therefore, the marginal *Enteromorpha* perennates by means of its buried fronds. In any case the capacity of the plants for regenerating new fronds from a tiny fragment of living cells is very surprising. One such fragment is seen in Fig. 5, *6*, which shows seven new fronds proliferated from a fragment consisting of very few cells.

IV. Another form of *Enteromorpha*, very different from any of the preceding, is the curled form shown in Fig. 4, *7–13*. This is to be found in masses on the soil between the grasses and other phanerogams in the *Glyceria*, *Aster-Glyceria* and *Obione* zones at Canvey, in the Juncetum zone and also sometimes on the marginal escarpment at Ynyslas. The masses are more or less firmly fixed in the muddy soil by a cement of silt, there being no attaching holdfast or rhizoids. Doubtless the fronds are carried up to these higher levels by tidal action and are stranded there. Because of the astounding vitality of these plants just referred to, the fragments remain alive for some time, and may get firmly fixed by silt deposited during subsequent tidal submergence. The fronds vary considerably in size, 1–8 mm. in diameter and up to 20 cm. in length. They are usually quite unbranched, and may either be simple or bear numerous proliferations. Sometimes the end of the frond is firmly rooted in the soil and the plant is more or less erect, but more often the filaments are looped, the loops being firmly caught in the mud at the base, the upper parts being free (Fig. 4, *12*). The larger plants are usually inflated and flattened alternately in a most irregular fashion. Where fixed in the soil the cells usually die, so that the frond in Fig. 4, *11* was found to consist of little more than a hollow dome, one layer of cells thick, fixed to the soil at the edges, the part of the original tube which lay in contact with the soil having completely decayed away.

It seems certain that the plants of type IV have developed from fragments of types I–III, which have been washed up by the tide and are struggling to keep up an existence under unfavourable conditions. Moisture is a problem in the higher zones where these plants are found, but the phanerogams provide considerable protection from desiccation. It would appear that the conditions even allow further development after the fronds are deposited, since it was found, after carefully washing away the soil from the mass figured in Fig. 4, *7*, that the slender curly fronds were really proliferated from fragments of larger tubes whose remains were hidden in the soil (Fig. 4, *9*, *10*). Here a tube 4 or 5 mm. in diameter had given rise to numerous fronds up to 2 mm. broad and 7 cm. long. Possibly the more slender forms of IV often arise from proliferating wider fronds in this way, but the stouter forms, such as are figured in Fig. 4, *11* and *12*, seem to be fragments which have persisted more or less in

the condition in which they were deposited. Their convoluted form is probably to be explained in part as in the case of A, by the cells actively growing and
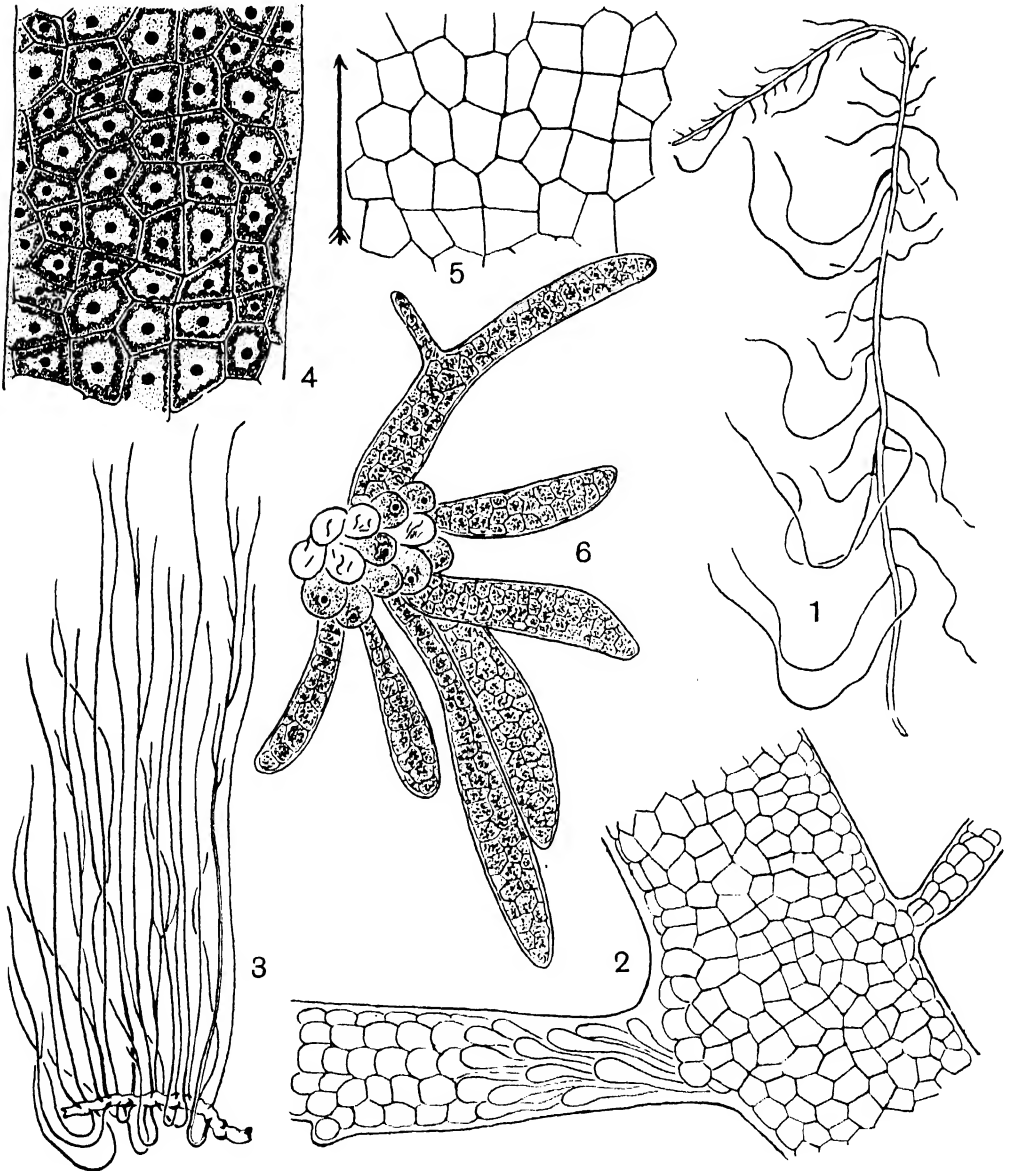
FIG. 5. *Enteromorpha ? prolifera* J. G. Ag. *1* and *3*, two examples, × 1; *2*, part of *1*, × 245; *4*, part of a branch of *1*, × 613; *5*, part of the main axis of *1*, × 613 (the arrow shows the longitudinal direction of the filament); *6*, a proliferating fragment, × 245.

expanding the area of the thallus, which, being firmly fixed at certain points to the soil, bulges in any possible direction to relieve the expansion.

The cells of type IV show slight differences as compared with the preceding types in relation to the much drier habitat. They are somewhat larger and more

polygonal (Fig. 4, *8*). Sometimes, probably as a result of extreme desiccation, the cells become more rounded in outline, and the walls relatively thicker, whilst the contents become very much denser (Fig. 4, *13*).

A certain peculiarity was noticed in B in many of the branching fronds. The cells near the base of a branch or proliferation frequently showed a strong tendency to develop filamentous outgrowths running backwards into the main filament, in a manner similar to that in which the holdfast is ordinarily formed in this genus (Fig. 5, *2*). In the plant shown as Fig. 5, *1*, all the larger branches showed this feature, but very often the more slender branches showed no trace of this peculiarity. Just as the character is not constant in the appendages of one individual, neither does it occur in all the specimens of one sample, and individuals showing the feature may occur alongside those which do not. On the other hand the majority of the individuals may show the character or *vice versa*. Thus it did not seem possible to correlate the peculiarity with any outside factor. That it serves a useful purpose is quite likely. The plants of *Enteromorpha* seem to depend for their existence on the salt marsh very largely on their great capacity for regeneration. The elongation of the cells at the base of the newly proliferated fronds may serve to weaken the attachment of the daughter filament to the original frond, so that it may easily be separated by the force of the tides and vegetative multiplication more readily effected.

<div align="center">CLADOPHORACEAE.</div>

9. Rhizoclonium hieroglyphicum (Ag.) Kütz. formae.

Canvey. A, B, C, and D. Probably present all the year round.
Ynyslas. A, B, C, D, E, and F. All the year round.   Fig. 6, *4–8*.

The forms of *Rhizoclonium* are very puzzling, but they are probably all forms of *R. hieroglyphicum*. The diameter of the filaments varied from 12 to 40μ, and the cells were from one to three times longer than their width. Forms as slender as 12μ were rare, the plants usually falling into three groups as regards size, 16–18μ, 20–25μ and 28–32μ, but not adhering rigidly to these dimensions.

At Canvey, all these three types occurred, but the largest was rather more common than the medium size and the smallest was seldom seen. Here, however, *Rhizoclonium* was rarely present in abundance, and it was particularly scarce in summer (May–September), becoming more prominent in winter. Its usual position is in the *Aster-Salicornia* zone, where it forms a thin weft over bare soil, or a more or less thick incrustation on the lower parts of *Aster* stumps. It is often present as an epiphyte on *Aster* stems when it is not present on the soil, and *Enteromorpha minima* is a common associate with it in this habitat. It may also be present in the festoons of algae which persist for so long on the remains of old *Salicornia* plants in the spring. The cells were usually as long as, or up to twice as long as broad, and rhizoidal outgrowths were frequently produced, especially in the case of filaments over 28μ in diameter (Fig. 6, *7*, *8*).

The separating wall at the junction of the rhizoid and the filament was often half pushed back into the supporting cell, or entirely pushed back (Fig. 6, 7). This is a character of *R. hieroglyphicum* subsp. *riparium*. The filaments frequently showed an attaching base (Fig. 6, *4*) and the apex was very characteristic, the cell wall being peculiarly thickened, giving a conical appearance to the apex (Fig. 6, *5*, *6*). On the whole, the Canvey representatives of this alga are fairly uniform and belong to the same form of the species. The presence or absence of rhizoidal branches was variable, but when the alga was present in any quantity they were usually to be found in some individuals. At Canvey, *Rhizoclonium* is not an important constituent of the alga flora, and is more often an epiphyte than a soil coloniser. The form in question here is probably subsp. *riparium* (Harv.) Stockm. (Heering (**29**), p. 21).

At Ynyslas, on the other hand, *Rhizoclonium* is the most important alga on the marsh. It is occasional at the margins, where, although it never establishes itself in a stratum on the shifting sand which is disturbed by the tide, it is sparse amongst the *Enteromorpha* tangles anchored on *Salicornia* plants, or lying free on the marginal strand. It also forms locally extensive continuous sheets covering the vertical faces of escarpments, and if, owing to undercutting by the waves, a piece of the marginal sod should fall to a lower level, it rapidly becomes clothed with *Rhizoclonium*. *Rhizoclonium* is certainly the stable inhabitant of the greater part of the marsh, and tends to extend into all spots not already occupied. Thus areas in any zone where the growth of phanerogams is prevented by the sheep which make definite tracks along the marsh, or by any other agency, become covered in time by *Rhizoclonium*.

In the turf zones *Rhizoclonium* is very general, and perhaps it is most abundant in the winter months. In the drier months of the summer Cyanophyceae make more headway and *Rhizoclonium* is less important. Nevertheless it withstands long periods of desiccation very well, and in such cases its cells become filled with the glistening globules described by Fritsch (**18**, p. 143). The alga does not flourish as well in the Upper Festucetum zone as in the lower zones. In the Armerietum and Lower Festucetum, the grasses usually grow so close together that the alga has not sufficient space to become conspicuous, but wherever space is available, it forms sheets 2 cm. or more in diameter, and 2–3 mm. in thickness. The stratum separates quite readily from the soil, so that the algal threads obviously do not penetrate very deeply into the substratum. The wad often separates easily into several horizontal layers which consist of pure *Rhizoclonium*. According to the time of the year, the different layers vary in degree of vitality. In the winter months the upper layers are active and have a normal appearance, whilst the lower ones are apparently resting, the cells having very dense contents with abundant oil drops. In summer the upper strata are often bleached and unhealthy, whilst the lower ones, protected from desiccation by the upper layers, are still green and vigorous.

In the Juncetum zone, since there is more space available on the soil between the *Juncus* plants, the alga often covers areas several centimetres in diameter. When thus growing actively with plenty of space available, as also on marginal escarpments, *Rhizoclonium* forms a sheet with a rippled surface, like crêpe. Possibly this raising of the surface is due to the intercalary growth of the filaments, which, anchored at various points, must bulge upwards as they increase in length.

The alga was very much more variable at Ynyslas than at Canvey, but it was very difficult to separate the forms as distinct types. Most abundant were filaments about 24–36μ in diameter, the more slender ones tending to have relatively shorter cells, up to twice as long as broad, and the coarser ones over 30μ being usually two or three times longer than their diameter. Rhizoidal branches, in contrast to the Canvey alga, were exceedingly rare, in spite of the great quantity of the material examined. Except for this feature the alga was very similar in the two marshes.

In August, 1928, large masses of *Rhizoclonium*, 3 or 4 ft. in diameter and several inches thick, were found lying in marginal creeks at Ynyslas, as if they had been washed in by the tide and stranded there (cf. Carter (**9**), p. 348). This mass, green and healthy, was almost pure *Rhizoclonium*, there being practically no *Enteromorpha* mixed with it. The threads were soft to the touch, and straight, not being crisped and crinkled as is so often the case in *Rhizoclonium*. The cells were 38μ in diameter, and about three times longer than their breadth. The filaments were very uniform and the cell contents showed a reticulate chloroplast with numerous pyrenoids. There was no trace of rhizoid formation in this mass. On no other occasion has *Rhizoclonium* been found lying in such quantity not attached to the substratum. It does not seem possible to separate this coarse form, which in the free mass never has rhizoids, from the form growing amongst the turf, which, on rare occasions, has exceedingly short rhizoids, not separated from the filament by a cross wall. Both should probably be placed under *R. hieroglyphicum* subsp. *typicum* Stockm. (Heering (**29**), p. 20). This form is characterised by the absence or poor development of rhizoids, but is usually reported from fresh waters.

In addition to these fairly stout forms of *Rhizoclonium*, two forms less than 20μ in diameter were encountered at Ynyslas. One, which varied from 16 to 20μ in diameter, was not infrequent, being often present in quantity in the Glycerietum and Armerietum and occurring at times with the coarser forms in the higher parts of the marsh. This form had cells 2–2$\frac{1}{2}$ times longer than broad, and rhizoidal branches were quite frequent, being usually, however, continuous with the main filament, with no separating wall, or separated by a simple straight wall, not showing the characteristic triangular cell at the base as in the Canvey form. At first it seemed natural to consider this alga as distinct from the coarser forms of *Rhizoclonium* at Ynyslas, from which it differs not only in its more crinkled and slender filaments, but also in its habit of

growth, the carpet formed by this alga being finer and more compact, and adhering more closely to the ground. Later, however, the two forms were found in organic connection with each other, in a filament which at the one end showed cells 28μ in diameter, 1–1½ times longer than broad, gradually decreasing in width to give at the other end cells only 18μ in diameter, and twice as long as broad. This showed that one would not be justified in separating the two forms. In its relatively simple rhizoids and proportionately longer cells this form, 16–20μ in diameter, is probably also nearer to subsp. *typicum* than to subsp. *riparium*.

Lastly, a very slender form of *Rhizoclonium* 10–12μ in diameter was observed on several occasions, on an escarpment between the Lower Festucetum and Armerietum zones and also in the turf of the Armerietum zone near the shore. This slender form had cells one to four times longer than broad, and there were very few or no rhizoidal branches. The cell wall was quite stout and the plants agreed fairly well with subsp. *Kerneri* Stockm. (Heering (29), p. 23), except that rhizoids are not recorded for this form. This alga is relatively rare both at Canvey and Ynyslas; on the former marsh it was only observed once, in the *Aster-Glyceria* zone.

The Ynyslas forms of *Rhizoclonium* differ from those at Canvey in several important respects: scarcity of rhizoids, absence of a basal attaching holdfast, and absence of a conical apex. It is possible that all these characters may be correlated with each other. The Canvey plants are usually epiphytes, erect plants attached by a basal holdfast which is adapted to hold the filament vertically (Fig. 6, *4*), and the apical cell differs from the intercalary cells morphologically. As the filament grows in length and is no longer able to hold itself rigid, it probably collapses on to the substratum, and develops other rhizoids which help to prevent it from being torn away by the force of the tide. The Ynyslas alga is always prostrate and grows in thick blankets on the substratum so that the threads mutually protect each other. It is impossible to find a basal attaching holdfast such as occurs in the epiphytic Canvey plants, and if one succeeds in finding a typical unbroken apex, it is seen that the end cell is merely rounded and not conical. Moreover if the end of a filament is modified for attaching, it merely sends out a simple rhizoid similar to that developed by intercalary cells, and never shows the true basal holdfast of the Canvey plant. Thus it would seem that the Canvey *Rhizoclonium* is primarily attached and erect, whilst the Ynyslas forms are prostrate and mat forming, and the differences in morphology can be correlated with the differences in habit.

Wille (51) has put forward the idea that the formation of rhizoids may sometimes be induced by chemical stimuli, as when filaments growing on damp ground send rhizoids down into it, or by mechanical stimuli, as when strong wave action causes the plant to anchor itself more firmly by rhizoids to the substratum. It does not appear that differences in moisture would account

for the greater development of rhizoids at Canvey, though possibly the more exposed position of the filaments, owing to a sparser habit of growth, may render the mechanical explanation more correct. Wille has further stated that in the subsp. *riparium* 2–4 pyrenoids are present in each cell. This has been repeated by Heering (**29**, p. 23). Obviously this number should not be taken as being correct for all forms of the alga, since a cell which measures $25 \times 50\mu$ will certainly contain many more.
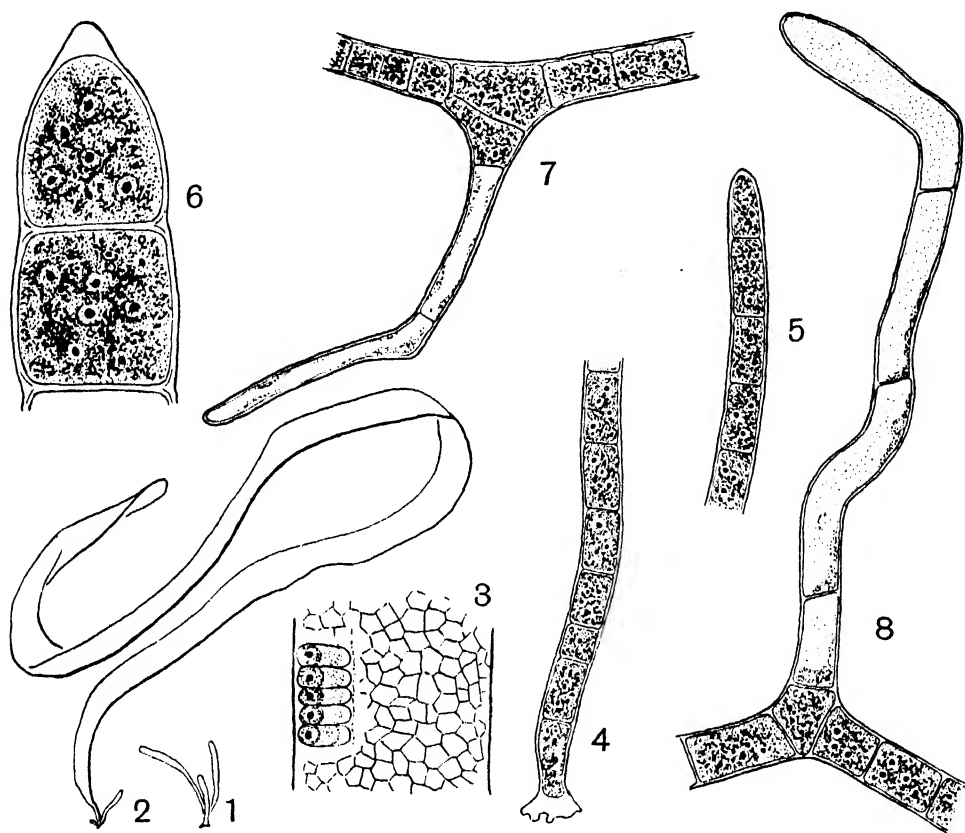
FIG. 6. Community No. V[1]. *1–3, Enteromorpha minima* Näg. *1, 2,* entire plants, × 16: *3,* portion of thallus, × 545, some of the cells seen in profile. *4–8, Rhizoclonium hieroglyphicum* C. A. Ag. subsp. *riparium*, Stockmeyer. *4,* basal attachment of filament; *5, 6,* apex of filament; *7, 8,* rhizoidal branches. *4, 5, 7,* and *8,* × 218; *6,* × 980.

10. **Cladophora pachyderma** (Kjellm.) Brand var. *tenuior* (Börg.) Brand in Heering, 1921, p. 31 (*Rhizoclonium pachydermum* Kjellm. var *tenuior* Börg.).

Canvey. B, C, and D. ɪ and v.

This form is one of the rare algae of the salt marsh, only being seen on two occasions, and the probability is that it does not play any important part there. Its general appearance is that of *Rhizoclonium*, and examined with a hand

[1] See Part III.

lens it has the crinkled habit of species of that genus. The plants were about 2 cm. long, unbranched for quite a distance from the base, then with a few short branches about two or three cells long, finally with a number of rather longer branches (rarely bearing short branches of the second order) some little distance from the apex of the filament. The insertion of the branches varied; sometimes they projected nearly at right angles from the main filament, and sometimes they showed almost normal "evektion." There always seemed to be a long unbranched apex to the plants.

The plants were occupying very different habitats on the two occasions on which they were found. On the first occasion they were growing in a trickle of tidal water flowing over a temporary dam of débris towards the sea, and the alga was afterwards found growing on the firm soil of the escarpment between the *Obione* and Upper *Glyceria* zones.

<div align="center">VAUCHERIACEAE.</div>

Vaucheria spp.
Canvey. A, B, and C. All the year round.
Ynyslas. A, B, C, D, E, and F.

Forms of *Vaucheria* were exceedingly abundant on both marshes. Unfortunately fruit was relatively rare, especially on the Canvey marsh, so that it is impossible to give the vertical distribution of each species with any degree of certainty.

At Canvey Island, the genus is rarely represented in either the *Aster-Glyceria* or the Upper *Glyceria* zones, probably because the frequent beating down of the tall grasses by tidal submergence renders illumination of the surface of the ground too feeble to support its growth. It is very important, however, at the upper margins of all channels, although not descending so far that it would come under the influence of every tide. It prefers the less disturbed regions which are not overshadowed by thick phanerogam growth, where it can readily be seen as a dark blue-green carpet, the siphons often standing erect like the pile of velvet. Growing as it does in the marginal zones, *Vaucheria* is probably of very great importance in helping to make the marginal soil firm, although it must frequently be washed away as the result of *very* strong erosion by the tides. A certain part of the *Aster-Salicornia* zone at Canvey, during the early part of observations there, was obviously silting up. *Vaucheria* finds such spots very favourable, and by its habit of growth probably increases the rate of sedimentation considerably by trapping particles in its upright pile. After a time, however, erosion started in this particular spot, and after about 9 months *Vaucheria* had entirely disappeared. Thus, although the alga is always associated with silting up, it is unable to withstand indefinitely the force of the waves.

The capacity of *Vaucheria* for binding soft mud was observed by studying samples of the surface soil in which it was vegetating actively. Where it is

growing vigorously, if one rubs the surface of the algal carpet in the field, a black coloration is obvious. This is due partly to inorganic black particles and partly to the blackened dead *Vaucheria* siphons which ramify in the underlying mud. The blackness is undoubtedly due to the presence of sulphides, as a strong odour of hydrogen sulphide is obvious, and moreover filamentous sulphur bacteria are commonly observed amongst the Cyanophyceae in the marginal regions[1]. The surface layer of soil was removed with as little disturbance as possible to a depth of about an inch from a pan which was obviously silting up, and bore a rich surface growth of *Vaucheria*. The strength of the *Vaucheria* carpet was tested by allowing a strong stream of water to fall on the under side of the sod from the tap. It was found that just beneath the surface, a black layer, 3 or 4 mm. thick, resisted the running water very effectively. This stiff layer owes its rigidity to the fact that the *Vaucheria* siphons are intricately interwoven in it, and the muddy matrix cannot be washed away. A vertical cut through the sod, carefully washed, showed that the black slimy *Vaucheria* siphons can be distinguished for at least 1 cm. beneath the surface, but apparently at this depth decay has advanced so far that the threads are unable to resist so great a pressure as the flow of water from a tap. The black layer near the surface which is so resistant is quite gelatinous in consistency. In other parts of the same pan, where colonisation had been in progress for a longer time, and *Vaucheria* had been in possession of the substratum for a longer period, the black resistant layer was as much as 2 cm. in

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[1]. **Ellis** (15) has investigated the cause of blackening of sand in the Clyde estuary, and came to the conclusion that the blackness was due to ferrous sulphide, which arises by the combination of the two elements, iron and sulphur. It was suggested by Ellis that the iron might arise by the activities of micro-organisms, which, operating on a compound of iron and organic matter, extract the organic material for their own use, and deposit the iron which usually becomes hydrated, forming ferric hydrate. Unfortunately the presence of such iron bacteria was not demonstrated by Ellis. The iron, according to Ellis, combines with the hydrogen sulphide produced by certain bacilli. The original source of the sulphur is not explained by Ellis. It was observed at Canvey that the mud itself becomes black, as well as the dead and decaying algal constituents. Sometimes the black appearance of the algae is due to the presence of black particles on the exterior of the walls, and sometimes the whole wall itself seems to be uniformly black all through. *Vaucheria*, *Enteromorpha* and Phaeophyceae all show the same thing. Microchemical tests showed that in all cases the blackness was accompanied by the presence of iron, the whole wall, if black, showing a deep blue coloration when tested with hydrochloric acid and potassium ferrocyanide. The addition of hydrochloric acid produces a strong smell of hydrogen sulphide, so that iron sulphide is indicated. Iron is very abundant in the mud, since it is sometimes deposited in a visible form on the walls of various algae, but it is difficult to explain exactly how this happens. As regards sulphur, it seems most likely to the writer that the dying algal protoplasm is the immediate source of this element. No doubt micro-organisms release the hydrogen sulphide, but the dying alga is probably the source. The reason why the blackness is not visible at the surface of the soil is that here the algae are actively growing and there is no great amount of organic sulphur available; but under the surface, where light does not penetrate, the algae become unhealthy and die, and this releases a lot of organic material with sulphur on which bacteria can operate. Hydrogen sulphide is undoubtedly generated in great quantities on a salt marsh. At Ynyslas large masses of drift algae are often deposited on the marsh and if these are disturbed a strong smell of hydrogen sulphide is evident. Drift algae in the pans soon die and become black in colour.

thickness, the upper 1 cm. containing abundant recognisable *Vaucheria* siphons. Some of these threads still had green contents, although they were already dead; the walls were sometimes colourless, but as a rule they were quite black. The lower centimetre of this black stratum had little recognisable alga and must depend for its tenacious nature on the colloidal material resulting from the decay of the filaments. The thickness of the black layer just beneath the surface was liable to local variation, but it evidently had some relation to the time that *Vaucheria* had been in occupation. Beneath the black layer the mud was pale brown in colour and sometimes formed brown pockets within the black mass itself.

These observations indicate that where *Vaucheria* is growing vigorously, it facilitates silting up, because, as the silt is deposited on top of it, the alga, which is very strongly heliotropic, is continually growing upwards. The amount of silt deposited at each submergence is not great, but nevertheless a visible brown film is deposited at each tide on the *Vaucheria* carpets. As the *Vaucheria* mat is growing upwards the older lower parts, which are being gradually but completely buried in the silt, die off, but the cell walls do not readily decompose, although the cell contents disappear. It is this great resistance of the walls to decay which makes the part of the sod just beneath the surface so tenacious, and renders *Vaucheria* an excellent alga for strengthening the margins of the channels.

At Ynyslas *Vaucheria* is a very important alga in all zones except the Upper Festucetum, which seems too dry for the alga to flourish, except in the damp winter months of the year. In general, *Vaucheria* is much more conspicuous in winter at Ynyslas, especially in the turf zones. In the Juncetum zones, however, *Vaucheria* persists in some abundance even in summer, evidently owing to the added protection of the tall *Juncus* haulms, which tend to maintain the humidity of the surface soil. *Vaucheria* sometimes occurs in sheltered marginal creeks, but, as a rule, there is too much disturbance here for the alga to exist. The marginal Glycerietum likewise seems to be too disturbed for the alga to flourish, and it is rarely found there in great quantity; but the inner zone of Glycerietum near the Juncetum provides a very suitable habitat. Owing to its lower level this zone is often very wet, and it is less disturbed than the marginal zones. The preference of *Vaucheria* for a moist habitat is proved by its vigorous growth near pans, especially those which remain full between successive submergences at high tide. Where it is thus flourishing, it can be recognised by its tightly packed erect filaments, conspicuous by their dark blue-green colour, emerging between the grasses. *Vaucheria* is also a general constituent of the Armerietum and Lower Festucetum zones. In dry weather *Vaucheria* tends to proliferate in a peculiar way, sending out short outgrowths at frequent intervals, which at first might be mistaken for developing sex organs (Fig. 7, *2*). Another peculiarity which may also be associated with drought conditions is the production of swellings at the ends of the

branches, and the separation of swollen vesicles at various points. In all these abnormalities there is no visible modification of the contents and no appreciable thickening of the cell wall.

At Canvey, also, *Vaucheria* tends to become less conspicuous in the summer months in the more exposed *Aster-Salicornia* zone, although it often persists in the marginal regions, probably because of the greater humidity of the soil, and also in the *Obione* zone because of the protection of the *Obione* plants, which keep the surface of the soil moist in the same way as *Juncus* at Ynyslas.

Probably at Ynyslas, *Vaucheria* does not play such an important part in stabilising the margin of the marsh as at Canvey. For the most part the Dovey soil has so little cohesion that the tidal waters cause erosion and undercutting
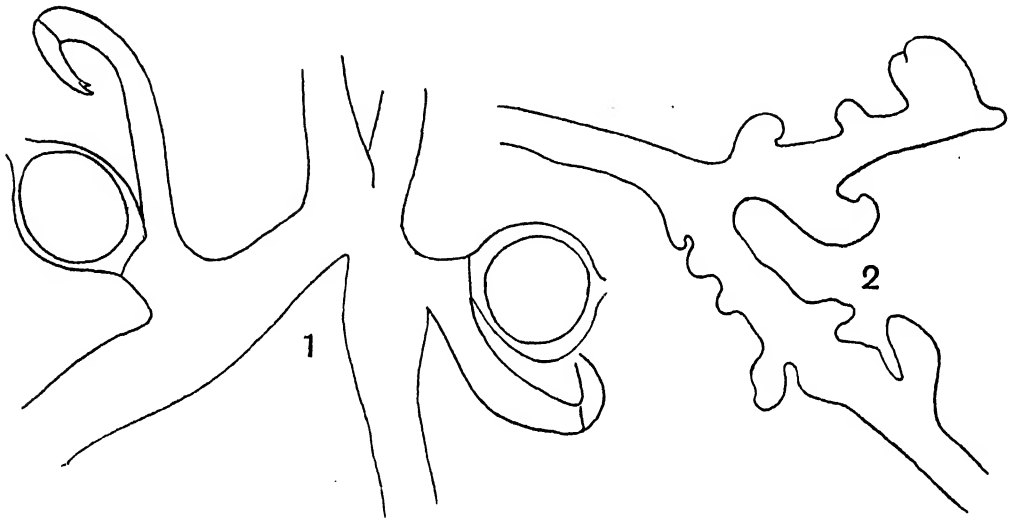
FIG. 7. *1, Vaucheria Woriniana* (Götz) Heering, × 97; *2, Vaucheria* sp., abnormality caused by drought, × 78.

of the turf, and these conditions *Vaucheria* is unable to tolerate. The vertical surface of escarpments resulting from such erosion has never been observed to become colonised by *Vaucheria*. The alga seems to prefer the softer mud of creeks and channels where in quiet places layers of silt are continually being deposited.

The following species of the genus have been observed in fruit:

11. **V. synandra** Woronin in Heering, 1921, p. 95, f. 86.

Ynyslas. F. IX.

The characters of the alga were quite typical. The vegetative filaments were about 60μ in diameter, the oogonia sessile with a conspicuous beak, and the oospores ovoid, about 100 × 130μ, a little flattened on the side of the beak. The oospore wall was pale yellow with rather broad, shallow depressions on the inner membrane. About four antheridia arose together from a single

supporting cell, separated from the thallus by a small empty cell. Very often, although not invariably, the antheridia and oogonia were on different filaments. This species must be one of the commonest on the Ynyslas marsh, since its oospores can frequently be found loose almost anywhere on the soil amongst other algae, and in September, 1926, practically all the samples of algae taken from any zone showed these oospores. Nordstedt (**36**) has observed that this alga occurs at fairly high levels on the shore. This is in accordance with the present observations, since it is always well above all ordinary high tides.

12. V. intermedia Nordst. 1879, p. 179.

Canvey. C. viii.
Ynyslas. Not observed fruiting, though slender vegetative filaments have been found which probably belong to this species. Observed fruiting at Glandyfi, about 4 miles further up the estuary, in the Lower Festucetum zone. ix.

The vegetative filaments were about 25–40μ in diameter. The oogonia terminate a short lateral branch, and the fertilisation pore is terminal. It is already known that gynandry is frequent in this species. Such monstrous forms were often seen amongst the fruiting specimens from these marshes, antheridia sometimes developing laterally from the oogonium itself. In rare cases one or two antheridia arose from the short stalk of the oogonium. There is always a small empty cell beneath the antheridium proper, and the latter opens by several pores. The oospores were about $90 \times 100\mu$, but completely ripe examples were not observed. This species is probably frequent in both marshes.

13. V. sphaerospora Nordst. 1878; Cooke, 1886, p. 219.

Ynyslas. Margin. iii.

The characters of this species are fairly constant. The sex organs are terminal on a long branch, and there is a septum in the branch some little distance from them. The antheridium terminates the branch, and is separated by an empty cell from the rest of the filament. The oogonium itself communicates by its very broad base directly with the segment isolated between the antheridium and the septum further back. A feature of the species is a conical empty space at the base of the oogonium (cf. Heering (**29**), p. 96, f. 89), since the oospore does not extend into the lower part. The oospores were about 120μ in diameter and their wall was very thin and colourless, although this may have been due to the fact that they were not properly ripe when observed. The species is known to be British, since it was recorded by Cooke (**13**) at low water on the Thames mud at Kew.

14. V. Woriniana (Götz) Heering, 1906, p. 165 (*V. geminata* Götz (in part), 1897, p. 126, f. 45).

Canvey. B. viii.   Fig. 7, *1*.

This alga is placed here with some hesitation, since as far as could be ascertained *V. Woriniana* has not hitherto been known from salt or brackish

localities, and moreover the oogonia usually appear to arise two or more together, whilst in the Canvey specimens there was usually a single oogonium in connection with each antheridium. In other characters, however, the alga seemed to agree.

The filaments were 60–100μ in diameter, and the sex organs were borne on a fairly long lateral branch. The oogonium was rather pear-shaped, with a terminal fertilisation pore, and arose about half-way along the branch. The rest of the branch was sharply hooked in the direction of the oogonium and at its tip a very short antheridium was cut off by a septum. Where details could be made out there seemed to be two openings to the antheridium. Fruiting examples were rare, and no fully ripe oospores were seen, although one specimen showed an oospore completely surrounded by a smooth membrane, measuring 150μ in diameter. *V. debaryana* Woronin (**52**) resembles the present form in its single oogonium and in the form of its antheridium, but differs in its smaller dimensions, and in its tendency to be encrusted with lime.

15. **V. Thuretii** Woronin in Heering, 1921, p. 83, f. 69.
Canvey. C. VIII.
Diam. fil. about 100μ; oosp. about 160 × 180μ.

The specimens were quite typical.

CHLOROCOCCACEAE.

16. **Chlorochytrium Facciolaae** (Borzi) Bristol.
Canvey. D. VI.
Ynyslas. E. Amongst Cyanophyceae and *Rhizoclonium*. Probably all the year round.

The cells were free amongst other algae, and never occurred in great quantity. They were usually about 45μ in diameter, with a firm cell wall and sometimes with a projecting peg. The alga has previously been recorded from marine habitats; nevertheless, the Upper Festucetum is probably less saline than the other zones of the marsh.

17. **C. Moorii** N. L. Gardner, 1917 (*Chlorocystis Cohnii* (Wright) Reinhardt in Collins, 1909, p. 148, f. 35).
Ynyslas. C. Epiphytic on *Enteromorpha percursa*. III, IX.

All stages in the development of this alga were observed, including the empty zoogonidangium with its open apex, the lid disappearing. The alga was entirely epiphytic, showing no tendency to penetrate its host.

CYANOPHYCEAE.

Thirty-seven species of Cyanophyceae are represented on the two marshes, about twenty-six occurring on each. The forms which occur at Canvey but not at Ynyslas include: *Oscillatoria laetevirens, O. nigro-viridis, O. brevis, O. formosa, Spirulina major, Pseudanabaena brevis, Plectonema Battersii, Merismopedia revoluta, M. mediterranea* and *M. convoluta*. Forms recorded from Ynyslas

but not from Canvey include *Rivularia* spp., *Nostoc commune, Lyngbya confervoides, Tolypothrix tenuis, Hydrocoleum lyngbyaceum, Phormidium molle* and *Gloeothece palea*. A survey of these facts leads one to the conclusion that the first group includes forms which are especially characteristic as blue-green sheets forming a covering on the sticky mud below the phanerogam limit, a type of habitat which does not exist at Ynyslas, owing to the shifting nature of the substratum; their absence is thereby explained. The second group of forms which do not occur at Canvey is seen to contain species which are characteristic of the Juncetum and Upper Festucetum zones and also marginal escarpments. The equivalents of the first two zones do not occur at Canvey, at any rate in the area examined, and escarpments are also very poorly represented, so that here again the facts are quite consistent.

The Cyanophyceae, on the whole, reach their highest development in late summer, July–October, and at this time of the year many species become very prominent which are exceedingly rare at other times of the year. Amongst these are *Anabaena torulosa, Nodularia Harveyana, Oscillatoria Bonnemaisonii, O. brevis, O. laetevirens, O. nigro-viridis, Phormidium angustissimum* and *P. foveolarum*. Besides this, many other species which are present in some quantity all the year round become more abundant then. On the other hand, there are a few forms, like *Nostoc commune* and *Rivularia* spp., which become most abundant in the wet winter months, November–March, and are less conspicuous in the drier months of the summer.

CHROOCOCCACEAE.

1. Gloeothece palea (Kütz.) Rabenh.

Ynyslas. C, D, E, and F. Probably all the year round. Fig. 12, 7.

This has not hitherto been regarded as a marine or brackish species, and indeed it is restricted to the highest zones of the marsh. The Juncetum seems to be its natural habitat, and here it grows in gelatinous masses on the bare soil, or adhering to *Rhizoclonium* or to larger Cyanophyceae. In late summer it may be found as low down as the Armerietum.

2. Chroococcus turgidus (Kütz.) Näg. in Geitler, 1925, p. 77, f. 71.

Canvey. D.

Ynyslas. B, near Juncetum. C. Occurrence sporadic.

Isolated specimens of this species were met with, but never large numbers. Its occurrence in the wetter Glycerietum near the *Juncus* zone at Ynyslas suggests that it prefers a moist habitat with little disturbance from tidal influence. It often occurred amongst *Vaucheria*.

3. Merismopedia revoluta Ask. 1894, p. 1, t. 1, f. 1.

Canvey. A, and D. In plankton of pans. Probably all the year round. Fig. 13, *1–3*.

Specimens of this alga were not uncommon as dark specks, if samples of marginal mud or Salicornietum were allowed to stand for a little time exposed

to the light. The colonies were up to $\frac{1}{2}$ mm. in diameter and were therefore easily visible with a hand lens. A very moist habitat is evidently necessary for this alga, for its position on the marsh is such that it is always kept moist by the tides, and moreover it is one of the few constituents of the plankton of pans. It never occurred in abundance.

The colonies were frequently rolled, or when very large, merely irregularly folded. The cells were about 4μ in diameter, nearly twice as long before division, and about 7μ in thickness (the diameter at right angles to the surface of the colony). The cells were rather compactly arranged, and narrow colourless gelatinous lines separated the small regular groups of cells, the sections of the thallus not being widely separated, although quite distinct. The cell contents were very faintly granular, and pale blue-green in colour. Askenasy says of his species that the colonies readily fall into fragments with slight pressure. This was not experienced with the Canvey material.

4. M. mediterranea Näg. 1849, p. 56 (*M. glauca* forma Geitler, 1930, p. 264).
Canvey. Plankton of pan. VI.   Fig. 13, *4, 5.*

This species had cells slightly smaller than the preceding, and its cell contents, although of the same colour, were quite homogeneous. The colonies were very much smaller, not coiled, and the limitations of each group of 16 cells much more definite, there being wider hyaline separating lines. The alga resembles *M. glauca* in all except size, the colonies always being larger than the dimensions usually given for that species. It seems to fall into Nägeli's species, which he described as marine from Naples, and which has not been recorded since so far as I know[1]. The alga was fairly frequent on the occasion recorded. Petersen (**40**) states that *M. glauca* is capable of withstanding considerable salinity, but gives no information concerning the size of the colonies.

5. M. convoluta Bréb. in Geitler, 1930, p. 262.
Canvey. A (Area No. 2 only). Rare. VIII.   Fig. 8.

Cells $4\cdot5$–5μ in diameter, spherical before division, elongated in the direction at right angles to the surface of the thallus to as much as 15μ.

This species seems to be distinct from all other species of *Merismopedia*. In its large rolled colonies it resembles *M. revoluta* Ask., but its exceedingly long cells (in the direction at right angles to the surface of the colony) prevent its being confused with any other. Early descriptions of the alga were not clear on this point, but Geitler has ascertained from authentic material that this is a distinctive feature of the species.

6. M. (Holopedia) sabulicola (Lagerh.) Kirchn. in Geitler, 1930, p. 267.
Canvey. A. Also in pans. I, II.   Fig. 13, *6–9.*

Although existing figures of this species are very poor, it seems probable that the Canvey specimens are identical with Lagerheim's alga. *The chief*

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[1] **Gardner** ((**21**), p. 239) has recorded *M. Gardneri* from the shores of California, and this, according to **Geitler** ((**24**), p. 265), is identical with Nägeli's alga.

difference seems to be in the habitat, since the salt-marsh alga was always free in the mud and not attached to sand grains like Lagerheim's original specimens. The colonies varied considerably in size and sometimes reached a diameter of 500µ.

The alga was never found in abundance, but seems to be a casual constituent of the soft mud bordering channels, or to live amongst filamentous diatoms or other epiphytes which festoon the submerged roots of grasses in the standing water of pans. Like all the other representatives of the genus *Merismopedia*, a moist habitat seems to be essential.
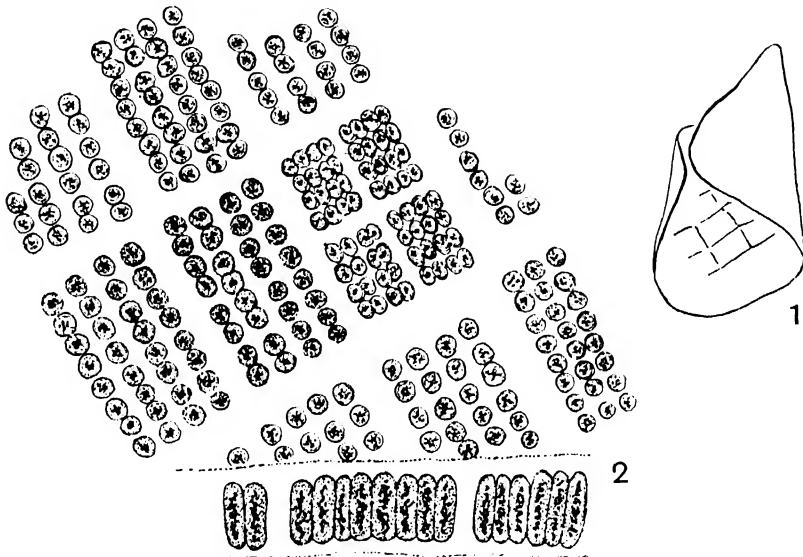
FIG. 8. *Merismopedia convoluta* Bréb. *1*, colony, × 109; *2*, × 613; part of the thallus is seen in profile.

OSCILLATORIACEAE.

7. **Oscillatoria Bonnemaisonii** Crouan.

Canvey. A, B, C, D, and E. VII–XI.
Ynyslas. B, C, D, and F. V–XI.   Fig. 9, *1–4*.

This seems to be a late summer and autumn form. It rarely occurs as a pure growth, being frequently mixed with *O. nigro-viridis* or *O. sancta*, or rarely as occasional isolated filaments scattered on bare soil. It has a wide vertical range, occurring from the margins up to the highest zones, although it undoubtedly reaches its best development in the *Aster-Salicornia* zone at Canvey. At Ynyslas it is not nearly so important. Here on one occasion it was found lining the bottom of a full pan. Thus its requirements as regards water are distinctly elastic.

The diameter of the filaments varied considerably (20–40µ) and on one occasion *hormogones were frequent (Fig. 9, 3, 4). The species seems to have the capacity for secreting a sheath, which is especially prominent when hormogones are being formed.

8. **O. brevis** Kütz. in Gom. 1892, p. 229, t. 7, f. 14, 15.

Canvey. C, and E. vi–ix.   Fig. 9, *5, 6.*

This form is placed here with some hesitation, since Geitler ((**23**), p. 371, f. 457), says the stratum formed by it is blue-green. At Canvey, the alga formed a dark, almost black stratum, and the colour of the filaments themselves was dull leaden grey. It is frequent in late summer beneath the *Obione* plants, either alone or with *Microcoleus chthonoplastes* or *Oscillatoria nigro-viridis*. It may be an important form on the escarpment from the *Obione* to the Upper *Glyceria* zone, or even in the Upper *Glyceria* zone itself. The cells were exceedingly short and the septa prominent.
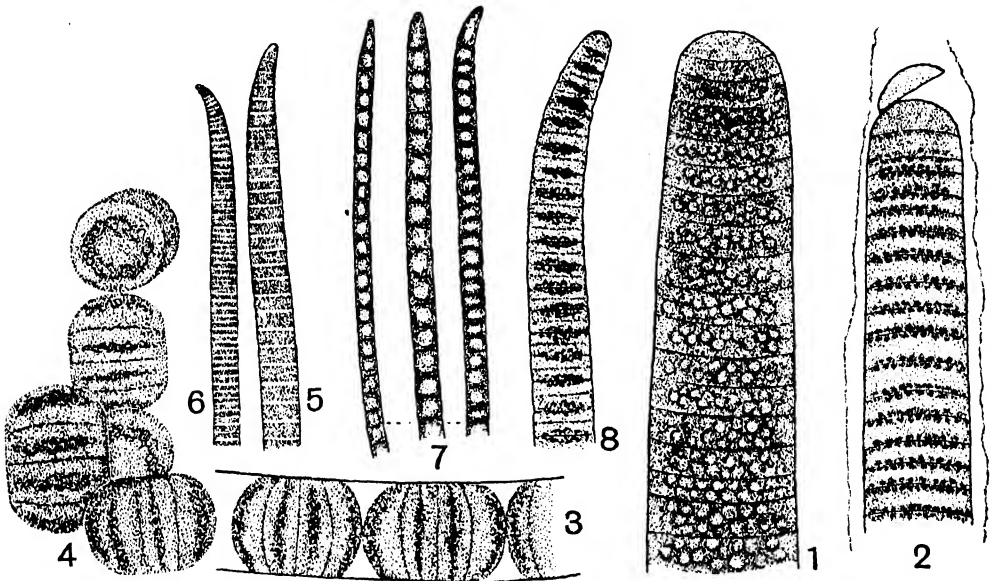
Fig. 9. Community No. VIII[1]. *1–4, Oscillatoria Bonnemaisonii* Crouan. Filament in *2* shows the secretion of a delicate sheath; *3, 4,* production of hormogones; *5, 6, O. brevis* Kütz.; *7, Phormidium autumnale*[2] (Ag.) Gom.; *8, Oscillatoria nigro-viridis* Thw. *3* and *4*, × 475 *5,* × 918; all others, × 552.

9. **O. corallinae** Gom.

Canvey. A, B, and D. All the year round.

Ynyslas. A, B, C, D, and F. All the year round.   Fig. 10, *13–15.*

This is one of the most constant algae found on the marsh. It can usually be found at any time of the year, especially in the lowest zones, but it occurs in greatest quantity in the late summer and autumn, July–November. It forms a large proportion of the stratum of Cyanophyceae which develops at this time of the year in the marginal regions of the marsh. In these films it is usually second in importance to *O. sancta,* and it may at times become dominant. The firmer and drier mud of the *Obione* and Upper *Glyceria* zones at Canvey do not seem to be such favourable habitats as the lower and moister

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[1] See Part III.   [2] Not invariably present.

zones. At Ynyslas it never has the opportunity of becoming such a conspicuous constituent of the marsh flora as at Canvey, but it is very general in the sheets of *Rhizoclonium* and *Enteromorpha percursa* and often occurs in great abundance amongst *Vaucheria*, both at Canvey and Ynyslas. It is rare at Ynyslas above the Lower Festucetum zone.

O. corallinae is certainly one of the algae most tolerant to frequent disturbance by tides, since it flourishes in the marginal zones at Canvey and Ynyslas. It is also a pioneer alga in silting localities (cf. also Carter (**9**), p. 366).

10. **O. formosa** Bory.

Canvey. A, and B. II–X. Fig. 10, *10*.

This appears to be a form which prefers the marginal mud, for it occurred in greatest abundance in the channels, where conditions are unsuited to the growth of phanerogams. It usually lives in association with other species of *Oscillatoria*, *Phormidium* and *Spirulina*, being sometimes present in quantity, although it is rarely the dominant form of the mixture. It is probably present during the greater part of the year, but is more prominent in September and October. It is one of the first colonisers on mud which is becoming stable, and is a common constituent in the flora of silting hummocks which occur in the larger channels. There have been a few previous brackish records for it.

11. **O. laetevirens** Crouan.

Canvey. A, B, C, and E. VII–XI. Fig. 10, *16*.

This is a somewhat rare form which never occurs in great quantity, but usually as isolated filaments amongst other Cyanophyceae. It is most likely to be encountered in the marginal zone or in the *Aster-Salicornia* zone, especially in late summer. It is less common in the higher parts of the marsh.

12. **O. nigro-viridis** Thw.

Canvey. A, B, C, and E. VII–I. Fig. 9, *8*.

Both Gomont (**25**) and Tilden (**48**, p. 69) give a maximum diameter for this species of 11μ, but the Canvey specimens were usually 13μ in diameter. The usual habitat for the species is in the higher parts of the marsh. It is most abundant in late summer, when, especially in the *Obione* zone, it frequently dominates, producing extensive brown films in which it may be pure except for diatoms, or it may be associated with *O. brevis*. At other times it occurs with *O. Bonnemaisonii* or *Microcoleus chthonoplastes*, and when it occurs in the Upper *Glyceria* zone it is frequently mixed with *Phormidium autumnale*. The cell contents are dull leaden grey in colour. It may persist in a fragmentary condition through the winter, but it is not found in spring.

13. **O. sancta** Kütz.

Canvey. A, B, C, and D. All the year round.
Ynyslas. A, B, C, and D. All the year round. Fig. 10, *11*, *12*.

Although this species is most abundant in the lower zones, it does not tolerate such moist habitats as *O. corallinae*, since, unlike that species, it does

not inhabit the almost liquid mud of the Area No. 2, though it is very abundant on any stretch of firm mud fringing the upper edges of the channels. It may be found at any rate to some extent in such habitats practically the whole year round, but in the late summer and autumn it is much more abundant and is the most important alga in the marginal stratum of Cyanophyceae (see also Part III).

14. Spirulina labyrinthiformis Menegh. in Geitler, 1925, p. 346.

Canvey. A. IX.
Ynyslas. C. Rare. VI.   Fig. 10, *4*

This tiny species was not common, but it is possible that it was frequently overlooked. Its trichomes are wound into a tight spiral, 1.5μ in diameter, with the turns contiguous. The diameter of the trichome was 0.5μ. It occurred with *Euglena* or with other Cyanophyceae on the marginal mud at Canvey, and amongst *Vaucheria* at Ynyslas.

15. S. major Kütz.

Canvey. A, and B. II–VIII.   Fig. 10, *2*.
Trich. 1.3μ diam.; spirals 2.5μ diam., turns 4.5μ apart.

This species, which is well known from both fresh water and brackish localities, was one of the commonest representatives of the genus on the marsh. It usually occurred with *Phormidium* and *Oscillatoria* spp.

16. S. subsalsa Oersted.

Canvey. A. Probably all the year round.
Ynyslas. B, C, D, and F.   Fig. 10, *1*.
Trich. $1.5–2\mu$ diam.; spirals contiguous, 4μ diam.

At Ynyslas this species usually occurred amongst *Vaucheria* between the phanerogams; at Canvey, on the marginal mud, where it was sometimes pure.

17. S. subtilissima Kütz.

Canvey. A, and B. VII–IX.
Ynyslas. A, B, and C. IX.   Fig. 10, *3*.
Trich. 0.8μ diam.; spirals 2μ in diam., turns 2.5μ apart.

This species was observed more frequently than any other. It was most abundant in the late autumn, especially amongst other blue-greens on the marginal mud at Canvey. At Ynyslas it was not so abundant, and was usually sparse amongst filaments of *Vaucheria* or *Rhizoclonium*.

18. Pseudanabaena brevis sp.nov.

Canvey. A. With diatoms in water from a pan. Probably all the year round.
                                                    Fig. 13, *10*, *11*.

Filamenta recta v. leviter flexuosa, stratum tenue cinereo-caerulescens efformantia, pigre prolabentia; cellulae prope sphaericae, post rapidam cellularum divisionem paulo minus longae quam latae, endochromate pallide coeruleo-viridi homogeneo, at centro dilutiore. Filamenta apicibus haud attenuata, cellulis apicalibus rotundatis et quam aliae aliquantulum amplioribus, vagina gelatinosa vix conspicua. Diam. fil. $3–4\mu$.

Habitat in stagnis et in limo molli, in aestuariis apud Canvey Island, Essex.

P. brevis, in its lack of heterocysts and slightly enlarged terminal cells, seems to be an independent form, remote from any known species of *Anabaena*
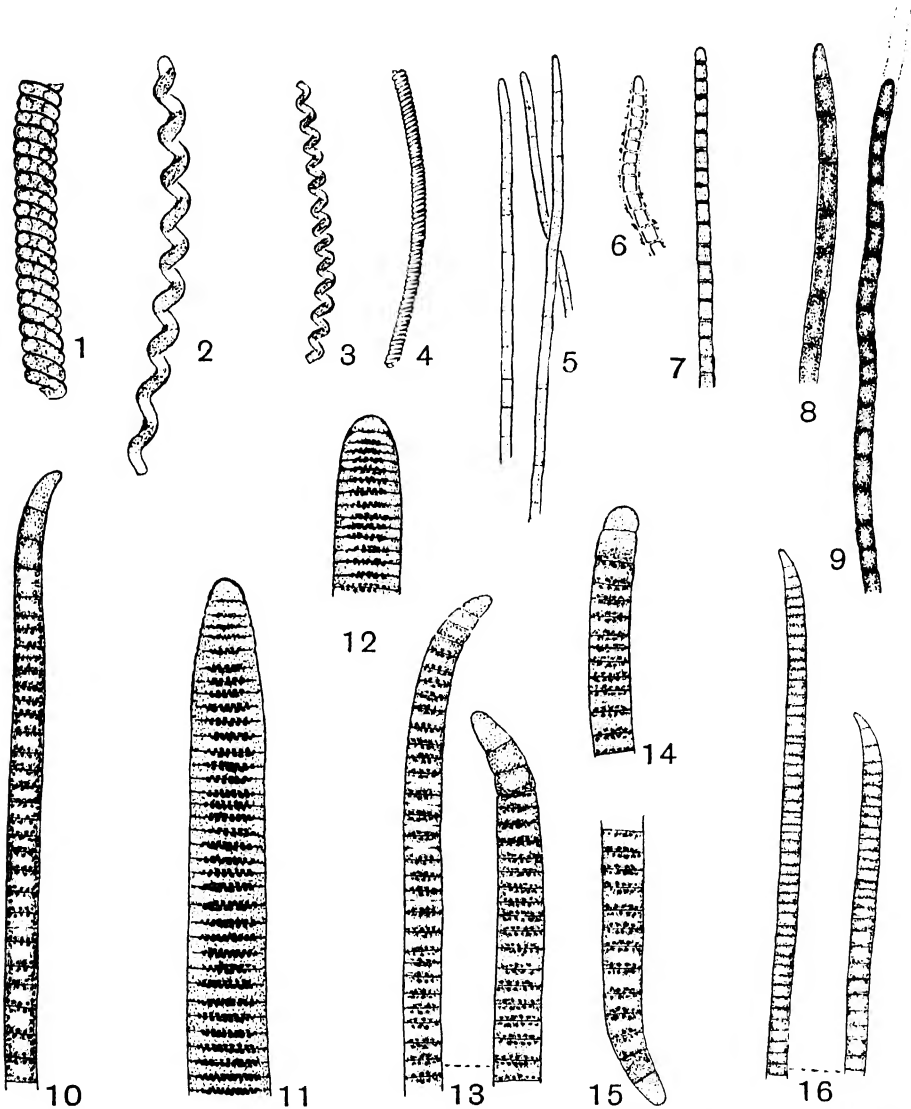
Fig. 10. Community No. III[1]. *1, Spirulina subsalsa* Oersted.; *2, S. major* Kütz.; *3, S. subtilissima* Kütz.; *4, S. labyrinthiformis* Menegh.; *5, Phormidium angustissimum* W. and G. S. West; *6, 7, P. foveolarum* (Mont.) Gom.; *8, 9, P. tenue* (Menegh.) Gom.; *10, Oscillatoria formosa* Bory; *11, 12, O. sancta* Kütz.; *13-15, O. corallinae* Gom.; *16, O. laetevirens* Crouan. *1-9*, × 1070; *10-16*, × 613.

or *Oscillatoria*. It differs from *O. lacustris* (Klebs) Geitler in its different habit, its smaller dimensions and its absence of pseudovacuoles or gas vacuoles. Its much shorter cells distinguish it from all other species of *Pseudanabaena*. It

¹ See Part III.

seems to be a natural inhabitant of the soft tidal mud, often occurring where there are no other Cyanophyceae visible, or where only *Microcoleus* spp. are present. Sometimes it produces a faint grey coloration on the surface of the brown mud, but quite often it is not visible at all in the field, only becoming apparent if a sample of the soft mud is allowed to stand exposed to light, when the greyish film rises to the surface. The filaments are quite free from each other; there is no apparent mucilage stratum, and only very rarely is a sheath secreted. There has been some suspicion that other species of the genus may possibly be developmental stages of other algae. *P. brevis*, however, seems to be constantly present on the marsh and to retain its definite characters. Whilst other species of the genus are found in such habitats that a saprophytic mode of existence is suspected, *P. brevis* occupies the same habitat as many other Cyanophyceae and diatoms and there is nothing to indicate that its method of nutrition is unusual.

19. **Phormidium angustissimum** W. and G. S. West.

Canvey. A, B, C, and D. vii–x.
Ynyslas. A, B, C, D, and E. vii–ix.　　　　　　　　　　　　　　　　Fig. 10, *5.*
Diam. fil. 0·6–1 μ; long. cell. 2–3·5 μ.

This narrow alga is referred to this species with some hesitation, since the previous records for it have all been fresh water. It was present in some abundance, forming a conspicuous sheet with other Cyanophyceae (mainly *Oscillatoria sancta*), especially in the late summer months in the marginal zone at Canvey. The filaments were long, and the cells three or four times longer than broad, the septa not being easily seen. The apical cell was very slightly attenuated, and rounded at the tip. The cell contents were pale blue, and practically homogeneous. The sheath was very delicate, not seen except where the trichome was broken, and not reacting with chlor-zinc-iodine.

20. **P. foveolarum** (Mont.) Gom.

Canvey. A, B, and C. vii–x.
Ynyslas. A, and E. vii, viii.　　　　　　　　　　　　　　　　　　Fig. 10, *6, 7.*
Diam. cell. 1·5–2 μ; long. cell. *ca.* 2 μ.

So far as I know, this species has not been previously recorded for a marine habitat. The filaments were not abundant and usually occurred in short lengths, in a blue-green sheet composed largely of *P. angustissimum* and *Oscillatoria sancta*. The sheath was not often visible except where the trichome was broken or when it became mucilaginous so that débris adhered to it. It does not become blue with chlor-zinc-iodine. A constant feature is the distinct separation of the cells. The apical cell is rounded and not at all attenuated. The cell contents are pale blue in colour.

21. **P. tenue** (Menegh.) Gom.

Canvey. A, B, C, and D. vii–x.
Ynyslas. E, and F. vi–vii.　　　.　　　　　　　　　　　　　　　Fig. 10, *8, 9.*
Diam. cell. 1·5–2·2 μ; long. cell. 2–3·5 μ.

This form has been recorded by Cotton (**14**), from brackish localities in Clare Island. It was often abundant at Canvey, especially in the marginal

film of Cyanophyceae which appears on bare mud in late summer. The sheath was not conspicuous and did not stain with chlor-zinc-iodine.

22. P. autumnale (Ag.) Gom.

Canvey. C, D, and E. Probably all the year round.
Ynyslas. C, D, and F. Probably all the year round. Fig. 9, 7.

This is a very characteristic alga of the higher zones, where it often forms a bright blue-green stratum. It is usually considered a fresh-water form, so that its restriction to the higher zones is understandable. The filaments varied from 3·5 to 5μ in diameter, and the apex of the trichome was very variable. As a rule it was slightly tapering and bent, and showed no very definite calyptra. At Canvey it occurred typically as a sheet overlying the prostrate grasses or the silt which covered them in the *Aster-Glyceria* or Upper *Glyceria* zones. In this habitat it was usually pure, but it might also occur sparsely with *Rhizoclonium* or *Vaucheria*. It also frequently formed pure sheets in the *Obione* zone, or covered the escarpment between this zone and the Upper *Glyceria* zone. At Ynyslas it was found forming a thin blue-green stratum on any bare spot between the phanerogams or on the escarpments.

23. P. molle. (Kütz.) Gom. 1892, p. 163, t. 4, f. 12.

Ynyslas. B, C, D, and F. Escarpments. Probably all the year round. Fig. 12, 3, 4.

This form is less common than the preceding, and was never observed on the Canvey marsh. It differed from Gomont's figure in the very slightly tapering apex. The filaments were sometimes aggregated in parallel groups or sometimes loosely entangled among other algae. The cells are about 3–4μ wide and about 1½ times as long; they are almost imperceptibly constricted at the septa, and have pale blue homogeneous contents. The sheath is very delicate, and is often difficult to distinguish. The alga is especially common amongst colonies of *Rivularia*, either on escarpments or in the turf zones.

24. Lyngbya confervoides Ag.

Canvey. B, and D. VIII.
Ynyslas. D, and F. IX. Fig. 11, 1, 2.

This species is a late summer and autumn form, whose appearance, at any rate on the Canvey marsh, seems to be rather sporadic. It occurs on this marsh in the middle zones, forming at times a distinct blue-green stratum of some extent in which occasional threads of *Oscillatoria formosa*, *Phormidium angustissimum* or *Microcoleus chthonoplastes* may occur. Owing to the great similarity of the trichomes of this alga to those of *Oscillatoria sancta*, there was great difficulty in distinguishing the two forms, especially as *O. sancta* seems capable at times of forming a very delicate colourless diffluent sheath. The sheath of *Lyngbya confervoides*, although colourless, is always firmer and stouter, and the apex of its trichome is blunter than the slightly attenuated apex of *Oscillatoria sancta*. Further the two forms are different ecologically. *Oscillatoria sancta* is the most important species in a stratum which appears in

summer and autumn in the upper parts of channels on the bare mud, or as high as the *Aster-Salicornia* zone, but in this stratum there are usually many other Cyanophyceae, including *Oscillatoria*, *Phormidium* and *Spirulina* spp. *Lyngbya confervoides* never seems to descend to the *Salicornia* or bare mud zones, and it often occurs pure or, if accompanied by other algae, these are small in quantity.
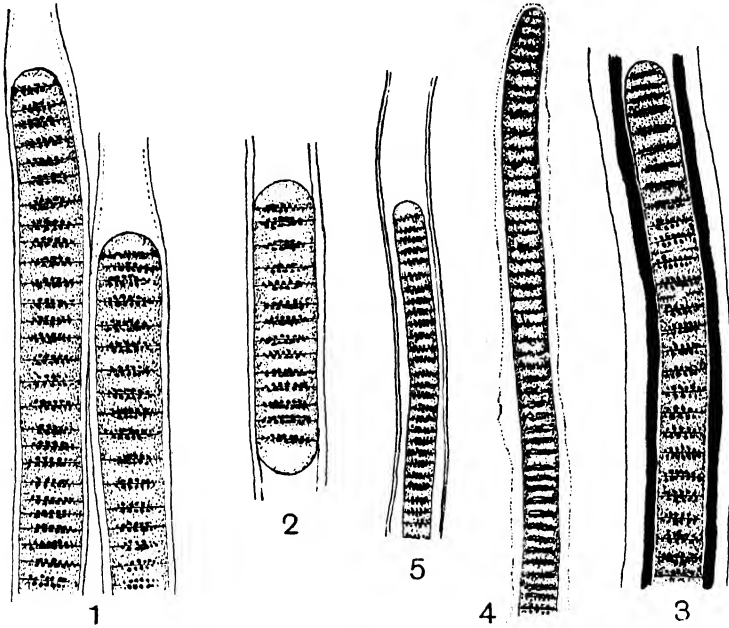
FIG. 11. *1, 2, Lyngbya confervoides* Ag.; *3–5, L. aestuarii* (Mert.) Liebmann. All × 613.

25. **L. lutea** (Ag.) Gom.

Canvey. C. VII.
Ynyslas. C, D, E, and F. All the year round. Fig. 12, *5, 6.*
Diam. fil. 4–7·5 μ; diam. trich. 3–6·5 μ; cells as long as, or rather longer than broad.

This species, which is very much more common on the Welsh marsh than at Canvey, shows considerable variation in size. There were two forms, which only differed in size and often occurred together. The smaller form had filaments 4 μ in diameter, and the septa between the cells were rather difficult to see, whilst the larger form reached a diameter of 7·5 μ, and had rather more conspicuous septa. Although occurring frequently with either *L. aestuarii* or *Phormidium autumnale* in a blue-green stratum covering bare soil between the phanerogams, perhaps its more characteristic habit took the form of a weft on the surface of the soil, frequently overgrown by threads of *Vaucheria* or *Rhizoclonium*. The blue-green mat is about 1 mm. thick, and the tortuous wavy nature of the filaments helps to make it more intricately interwoven. It is also common on the marginal escarpments or along the margins of pans. Its position on the marsh indicates a preference for the higher and less disturbed portions of the marsh.

26. **L. aestuarii** (Mert.) Liebmann.

Ynyslas. B, C, D, and F. All the year round.   Fig. 11, 3–5.
Diam. fil. 10–24 μ; diam. trich. 6–10 μ; cells 3–4 μ long.

This species does not occur as a conspicuous constituent of the Canvey marsh, in the particular parts investigated, and there is only one doubtful record for it from the submerged grass roots in a full pan. Possibly this may have been *L. confervoides*, which is a more frequent inhabitant of this marsh[1]. At Ynyslas the species was often represented by quite typical filaments showing the usual thick gelatinous sheath with the inner layers much darker and of a rich brown colour. The septa of the trichomes were usually conspicuously granulate. The species is a very common one on the Welsh marsh, and its distribution there approximates to that of *L. lutea*. It is rare at the margins of the marsh, but is much more abundant at higher levels, often forming, especially in the late summer and autumn, a pure stratum on any small bare area between the flowering plants in the Lower Festucetum or Juncetum; or it may be associated with *Microcoleus chthonoplastes* or other Cyanophyceae, *Vaucheria* or *Rhizoclonium*. The Upper Festucetum does not seem to be a suitable habitat either for this or the preceding species, being probably too dry.

27. **Hydrocoleum lyngbyaceum** Kütz. in Gom. 1892, p. 337, t. 12, f. 8–10.

Ynyslas. D, E, and F. v–ix.   Fig. 12, 8–10.
Diam. fil. 18–30 μ; diam. trich. 10–14 μ; cells 1–2 μ long.

This species is very characteristic of the Upper Festucetum zone, where it is frequent in late summer and autumn forming a stratum scrambling over mosses, sometimes pure, sometimes with other Cyanophyceae or Chlorophyceae. The trichomes are often seen without their sheath, when they might easily be mistaken for an *Oscillatoria* sp. When typical the trichomes are provided with a broad, colourless gelatinous sheath, the inner part of which is quite firm and lamellose, whilst the outer part seems to be more diffluent. There may be only one trichome in each filament, or several trichomes may adhere in a common envelope. The end of the trichome was sometimes only gradually rounded, but often was provided with a blunt or conical cap cell.

28. **Microcoleus acutirostris** Gom. 1892, p. 352.

Canvey. A, and B. All the year round.
Ynyslas. A, and B. ix–xi.   Fig. 13, 12–14.

The filaments were about 70–90 μ in diameter, containing about eight or more trichomes aggregated in the middle, so as to leave a thick colourless gelatinous surrounding zone. The trichomes were about 10 μ in diameter, greyish blue-green in colour, and had very granular contents. The apex is gently tapering to a rather acute tip. The cells vary somewhat in length, but are usually less than half their diameter.

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[1] At the same time it is an open question whether *L. aestuarii* and *L. confervoides* are specifically distinct, since they differ only in the colour of the sheath.

Unlike *M. chthonoplastes*, this species is distinctly limited in its distribution on the salt marshes, only occurring in the marginal zones. It is rarely apparent in the field, but will rise to the surface of the sample on standing (cf. also Carter (**9**), p. 354).
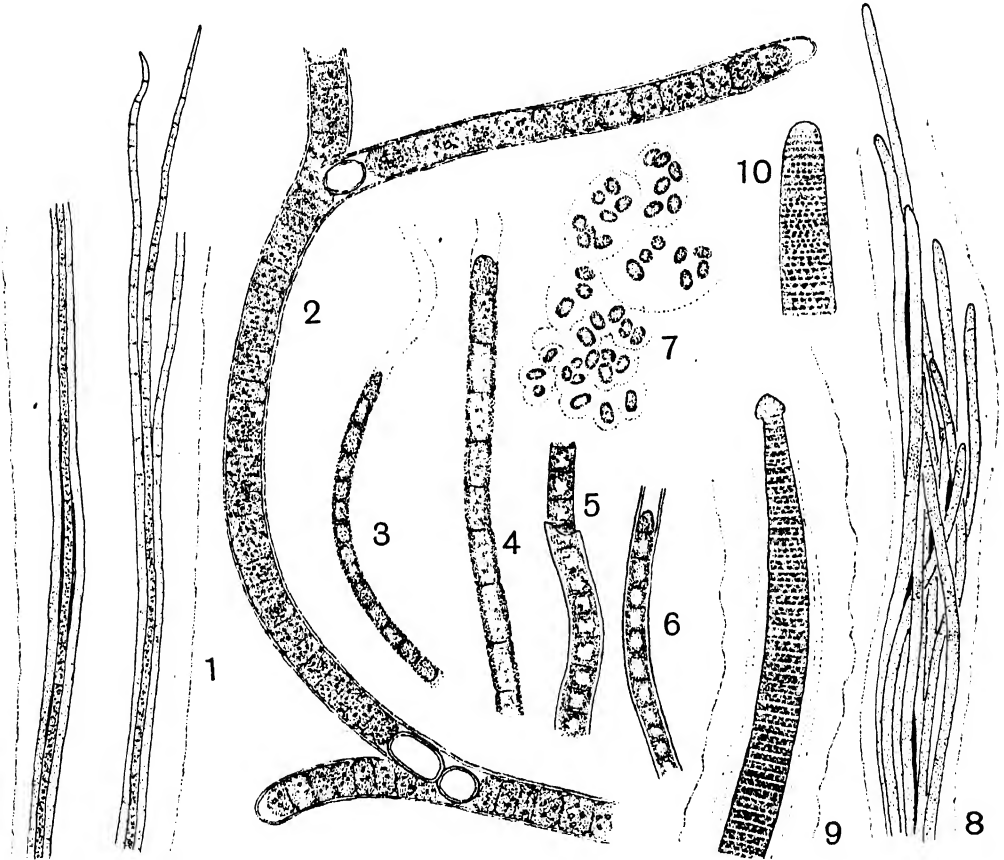
FIG. 12. Cyanophyceae characteristic of the higher zones at Ynyslas. *1, Microcoleus tenerrimus* Gom.; *2, Tolypothrix tenuis* Kütz.; *3, 4, Phormidium molle* (Kütz.) Gom.; *5, 6, Lyngbya lutea* (Ag.) Gom.; *7, Gloeothece palea* (Kütz.) Rabenh.; *8–10, Hydrocoleum lyngbyaceum* Kütz. *4*, ×971; *8*, ×218; all others ×545.

29. **M. chthonoplastes** Thur.

Canvey. A, B, C, D, and E. All the year round but more abundant VII–IX.
Ynyslas. A, B, C, D, E, and F. All the year round but more abundant VII–IX.

Fig. 13, *15–17*.

This is one of the most important algae on a salt marsh, as it is present at all times of the year and occurs at all levels. It is sparse in the marginal mud below the phanerogam zones and often rises to the surface of samples taken from this region. At times it may even produce a visible film on the surface mud, but, as a rule, such marginal films of Cyanophyceae seen in the field are due to *Oscillatoria* or *Lyngbya* spp. In higher zones, where the soil is firmer, the threads of the alga may be so close together that they give a dark blue-black

coloration to the surface soil. Blue-green films due to *M. chthonoplastes* can be distinguished with a hand lens in the field from those produced by *Oscillatoria* or *Lyngbya* spp., because even under low magnification the streaky nature of the growth is obvious, the result of the coarse bundles of trichomes characteristic of this species.

The alga reaches its greatest development July–September, when it often covers extensive areas in every zone, especially the *Aster-Salicornia*, *Obione* and *Glyceria* zones at Canvey. At Ynyslas there is rarely sufficient bare soil for the alga to become conspicuous in the same way, and here it usually occurs amongst *Vaucheria*, other algae or mosses, although if a bare spot should happen to occur it may be clothed with *Microcoleus chthonoplastes*. Such bare areas are frequently found on escarpments, or around the margins of pans, and here this alga is almost certain to be found. The alga is so general in the late summer that even if it does not occur in pure growths it is present amongst other algae, e.g. *Oscillatoria sancta*, *Anabaena*, *Nodularia*, *Phormidium autumnale*, etc. In winter and in spring, although it is not entirely wanting, it is reduced in quantity, and while it may not be encountered in all zones, it is likely to occur in the *Aster-Salicornia* zone at this time.

30. **M. tenerrimus** Gom. 1892, p. 355, t. 14, f. 9–11.

Canvey. C, escarpment to E. vii–ix.
Ynyslas. E, and F. i, iii, vi, viii. Fig. 12, *1*.

This species is very inconspicuous, never being recognisable except by microscopic examination. It rarely occurs with other species, and is never found in quantity. Where apparently bare soil occurs between other plants, careful examination often reveals its presence. There seems to be little doubt that *M. tenerrimus* prefers the upper levels and open situations. Thus it occurs in the Juncetum at Ynyslas, where there is much bare soil between the plants. It is not found amongst the matted dead haulms of *Glyceria* at Canvey, but it has occasionally been found, wherever there is a stretch of bare soil, on the escarpment to the *Obione* zone below.

NOSTOCACEAE.

31. **Nostoc commune** Vaucher.

Ynyslas. E, and F. All the year round.

Nostoc is a very conspicuous constituent of the Upper Festucetum zone, where it is usually visible in the field, especially in the damp winter months, as large soft gelatinous masses. It persists also in the summer months, but since the weather is drier it is only represented then by dry black shrivelled particles adhering to the soil, mosses or other plants. Very small colonies, discovered only by microscopic examination, have also been frequently found, especially in the summer months. Germinating hormogones, as figured by Geitler (**23**), have also been observed.
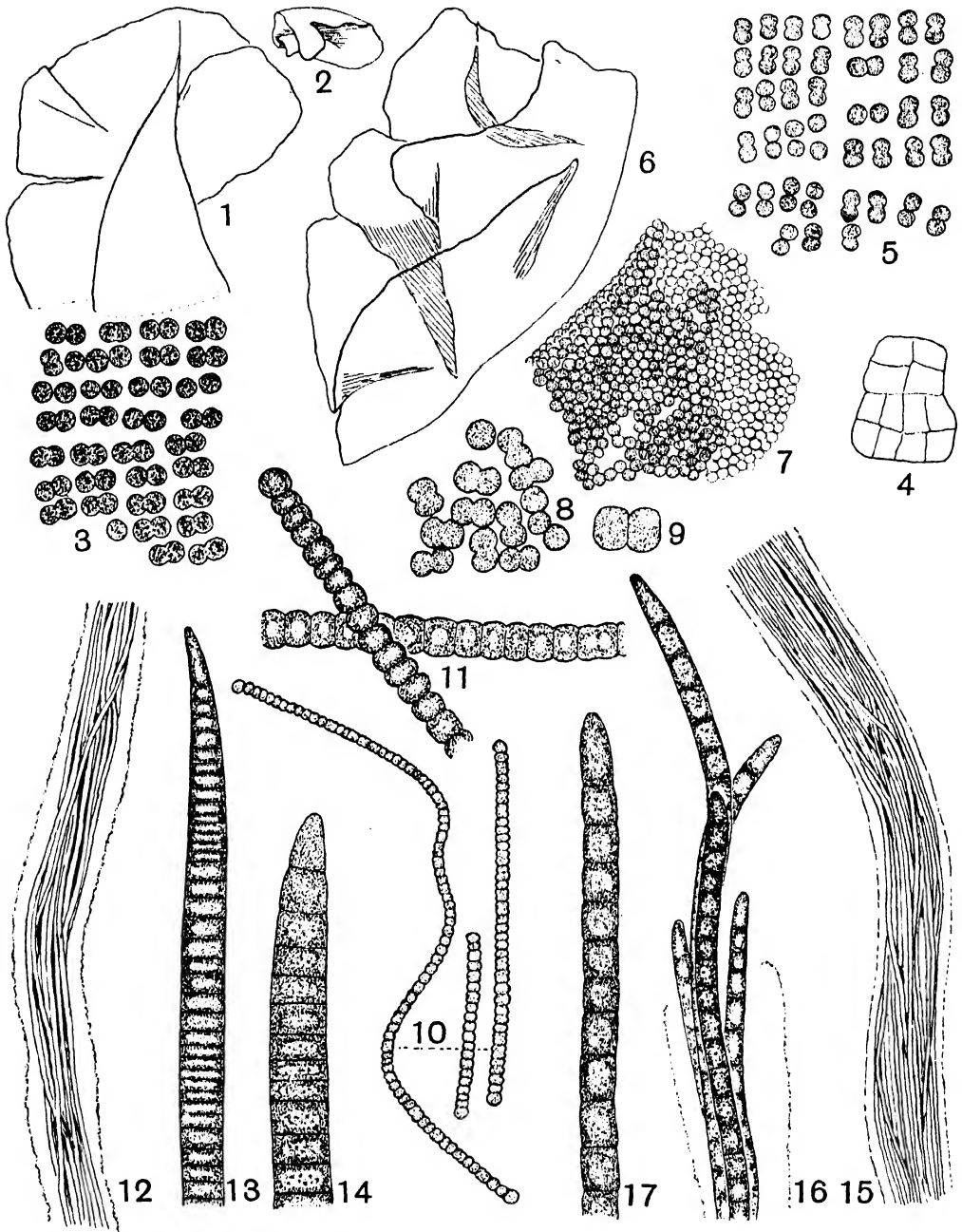
Fɪɢ. 13. Cyanophyceae of community No. 11[1]. *1–3, Merismopedia revoluta* Ask.: *1*, part of a large colony; *2*, smaller colony; *4, 5, M. mediterranea* Näg.; *6–9, M. (Holopedia) sabulicola* (Lagerh.) Kirchner: *6*, large colony; *7*, a portion of the folded colony, showing spaces between the cells; *8*, some of the cells in surface view of the colony, in active division; *9*, cells seen in the edge view of the thallus; *10, 11, Pseudanabaena brevis*, n.sp.; *12–14, Microcoleus acutirostris* Gom.; *15–17, M. chthonoplastes*. Thur. *1, 2, 4, 12,* and *15,* ×98; *6,* ×162; *7,* ×460; *8, 9,* and *11,* ×918; *14,* ×947; *17,* ×720; all others, ×552.

[1] See Part III.

Young colonies have a thick, firm cuticle, and in such plants the individual sheaths of the trichomes are not visible, and the jelly is colourless. In older colonies the firm cuticle disappears, and at the periphery the individual sheaths become apparent, often being coloured distinctly yellow.

32. **Anabaena torulosa** (Carm.) Lagerh.

Canvey. B, C, and D. vii–ix.
Ynyslas. E. Also along the margins of channels and in the plankton of a pan. vii, viii.

Fig. 14, *1–3*.
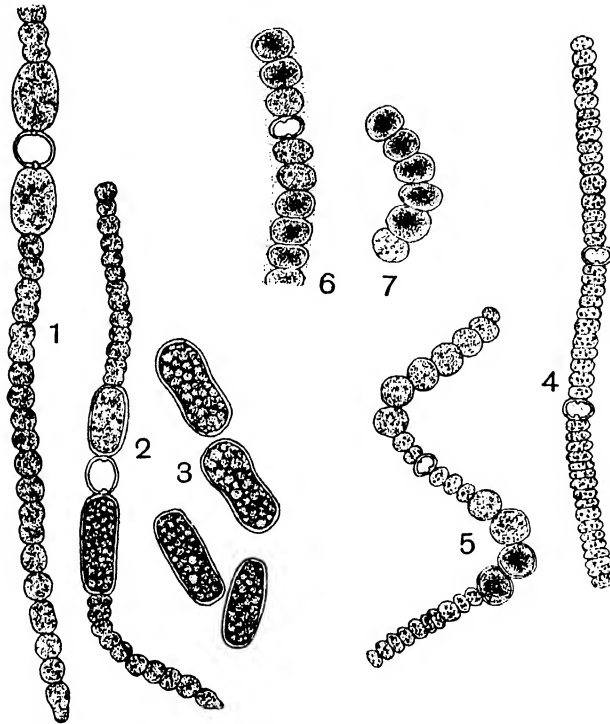
FIG. 14. Community No. VI[1]. *1–3, Anabaena torulosa* (Carm.) Lagerh; *4–7, Nodularia Harveyana* (Thw.) Thur. *1*, ×800; *5*, ×520; all others ×613.

This is a conspicuous late summer form which becomes very abundant from July to September and is absent during the rest of the year. It occurs at the margins of the channels at Canvey, but not on the softer mud, forming as a rule conspicuous bright blue-green circular colonies on the firmer soil near the *Aster-Salicornia* zone. These colonies, which vary in size from half an inch to several inches in diameter, are also general throughout the *Aster-Salicornia* and *Aster-Glyceria* zones. Even in the *Obione* zone it may at times be the dominant alga, but it has never been observed in the *Glyceria* zone. It spores abundantly in August and September, when pure masses of spores are often collected which might be easily mistaken, in the absence of vegetative filaments, for a unicellular form.

[1] See Part III.

At Ynyslas the shifting marginal sand and well-vegetated turf apparently do not offer such suitable habitats for the species, but in some sheltered channels in July its presence was denoted by the familiar brightly coloured patches. It also reached unusual abundance on one occasion as a bloom floating in the warm water of a pan in the Juncetum zone in July (cf. (9), p. 360).

33. Nodularia Harveyana (Thw.) Thur. in Born. et Thur. 1876, p. 122, t. xxix.

Canvey. A, and B. In pans. vii–x.
Ynyslas. C, D, and F. v–viii.   Fig. 14, *4–7*.
Diam. cell. veg. 4–4·5 μ; long. 3 μ; diam. heterocysts 5 μ; long. 3·5 μ; diam. spor. 6·5–8 μ; long. 5–6 μ.

This is a distinctly late summer form, like the preceding, with which it is frequently associated. It is best developed in the *Aster-Salicornia* zone at Canvey, where it forms at times large pure areas which may also spread over *Vaucheria* or *Enteromorpha*. At Ynyslas it does not as a rule form such extensive patches, but at the same time it is not uncommon. It spores freely July–October.

The descriptions of this alga given by Tilden (**48**, p. 183) and Forti (**17**, p. 432) are very misleading, since they indicate that the cells before division are as long as, or longer than broad. The same is true of Thuret's original description of the alga, which is evidently erroneous, as the figures in Bornet et Thuret (**5**) show an alga almost identical with the Canvey and Ynyslas salt-marsh forms. The only difference seems to be that the heterocysts are slightly larger in the British alga and also the wall of the spore is colourless, whilst the French specimens had a distinctly yellow wall. Possibly the spores observed by me were immature.

<center>SCYTONEMACEAE.</center>

34. Plectonema Battersii Gom. in Forti, 1907, p. 495.

Canvey. A, epiphytic on *Enteromorpha*. iv.

This was only found on one occasion, but it may sometimes have been overlooked. It certainly has no important rôle on the salt marsh. It is a well-known marine species.

35. Tolypothrix tenuis Kütz. in Forti, 1907, p. 545.

Ynyslas. E, and F. i, vii.   Fig. 12, *2*.
Filaments 9 μ diam., trich. blue-green, 6 μ diam.; sheath thin, firm and colourless; cells scarcely constricted except at the apex of the trichome, apical cell rounded; branches short, often on alternate sides of the main filament, with two heterocysts (or rarely one) at the base.

This alga, only observed on two occasions, both in some abundance, is referred to this species with some hesitation. Petersen (**40**) has described a forma *terrestris* from Iceland, but the Ynyslas alga is referred to the typical form, with which it agrees in size and other features. Petersen states (**40**, p. 305) that the typical form is capable of thriving on land, and that it is also

known from brackish water. Its occurrence on the highest zones at Ynyslas should therefore not occasion much surprise. It was found on bare soil, and was scarcely visible in the field.

RIVULARIACEAE.

36. **Rivularia atra** Roth in Fremy, 1927, p. 192.

Plants spherical, 1–4 mm. across, solitary or confluent to form large masses, 2 or 3 cm. across.

37. **R. nitida** Ag. in Fremy, 1927, p. 192.

Plants ½ to 2 cm. in diameter, often hollow, and flattened into a somewhat auricula e form. Ynyslas (both species). C, D, E, and F. Also all escarpments and margins of pans. All the year round.

Rivularia atra is much more abundant than *R. nitida*, though the latter was observed on three occasions in the Armerietum and the Juncetum. The genus is represented at all times of the year, but the plants are particularly flourishing in the winter months, when they are present in large quantity as small, very hard, round colonies, especially on the vertical faces of escarpments and at the margins of pans, where there is plenty of bare soil not colonised by phanerogams. At this time of the year it also tends to spread whenever possible between the grasses and other plants of the Armerietum or other turf zones, starting from escarpments or pan margins.

In the summer months the plants become shrivelled and less conspicuous and, especially in times of drought, they may be completely overlooked owing to their being covered with a thin white powdery deposit. This deposit was investigated chemically, both before and after incineration to destroy organic matter. It was found to be insoluble in concentrated sulphuric and acetic acids, proving the absence of carbonates. It was also insoluble in hot concentrated hydrochloric acid, but partially soluble in dilute nitric acid. The addition of ammonium oxalate to this solution gave a slight precipitate of minute crystals. This indicates that the original deposit contained calcium sulphate. The insoluble residue is probably silica.

In November, 1927, *R. atra* was observed to be forming hormogones in large quantity. Some of the colonies were covered with a pale green moist film, which, when scraped off, was found to contain numerous hormogones amongst débris.

At certain times of the year the *Rivularia* colonies seemed to be penetrated by a green alga belonging to the genus *Endoderma* (see p. 132).

Rivularia seems to be intolerant of standing water, or of too frequent submergence. Thus it is always found fairly high up on the marginal escarpments, on the firm border which often bends over from the horizontal zone above; and when growing around the margins of pans it is always well above the level of the standing water of the pan.

The colonies are exceedingly hard and are often partially embedded like jewels in the firm silt of the escarpment, so that the tiny spheres are only dis-

placed with some force. In winter, the colonies become so numerous that they tend to form concrescent masses in which individual colonies are difficult to see. A visit to the marsh in November, 1927, after an unusually high tide, showed that the *Rivularia* covering is very valuable in protecting the margins of the escarpments, since certain areas well clothed with *Rivularia* were not eroded, whilst adjoining portions of the escarpment had been so eroded as to expose freely the roots of grasses and other plants. Continual erosion, however, proves too severe for the alga, for when observations were made in March in the following year, it was found that erosion of the marginal escarpments and pans in the vicinity had resulted in the destruction of nearly all the *Rivularia* colonies, although further back in the marsh the plants were just as abundant as ever.

BACILLARIALES.

The diatoms occurring on both marshes were rarely present in sufficient quantity to be collected and cleared in the usual way by boiling with nitric acid. They occurred most abundantly at the margins of the marsh at Canvey, forming a brownish film, usually distinctly visible, on the soft substratum. Fairly pure samples could be obtained in such a case, but the proportion of mud was always high. At Ynyslas the more sandy and less tenacious marginal mud is not sufficiently stable for such a stratum to hold together, but in the more sheltered channels a film of diatoms is often apparent, and here many forms commonly found at the margins of the Canvey marsh are to be recognised. In all other zones of the marsh, however, diatoms rarely formed a visible film, but occurred more often as scattered individuals on the surface of soil which is apparently bare, or amongst Cyanophyceae or Chlorophyceae. Samples taken from such material contained so few diatoms that the risk of loss on boiling in nitric acid would have been very considerable. Samples were therefore spread on a slide and incinerated by heating over a Bunsen burner. By this treatment there was no danger of losing any individuals, either by reason of small size or delicate silicification. The last character is probably of importance in the case of poorly silicified species such as *Amphora lineolata* and *Nitzschia epithemioides*.

More than eighty species of the group have been identified, the majority of which are present on the Canvey marsh. The marsh at Ynyslas does not seem to be so rich in species, only about fifty species being recognised.

As regards the distribution of the diatoms over the marsh the zonation shown by the phanerogams is reflected to a slight degree in the diatom flora, though there are a few species which seem indifferent to the varying conditions of exposure and submergence at different levels and are to be found in all zones. The zonation in the diatoms is more apparent at Canvey than at Ynyslas. Seasonal periodicity involving a difference of species at different times of the

year was only striking in the lowest or marginal zone. Here there were, in addition to the forms which occur at all times of the year, certain others which become especially prominent either in the summer or winter. This periodicity may be more prominent in the marginal zone than elsewhere because the stratum of diatoms is much more abundant there and covers considerable areas without interruption. Any sample taken is thus fairly typical of the whole. In the higher zones other algae and phanerogams interrupt the distribution of the diatoms, so that the chances of taking an average sample are not so great. Forms relatively rare in one spot might be common elsewhere. In this way periodicity might easily be obscured.

From records taken at Canvey it seemed possible to distinguish the following groups. In each group rare species have been excluded and the grouping should be regarded as approximate rather than rigid.

I. *Occurring in all zones* (Fig. 15). *Navicula gregaria, N. pygmaea, N. subinflata* var. *elliptica, N. vacillans, N. didyma, N. cincta* var. *heufleri, Gyrosigma Spenceri, Stauroneis septentrionalis* and *Nitzschia navicularis*. This list includes only those which are to be found in fair quantity in any zone and do not seem to be specially abundant in any particular one.

II. *Top zones* (*Obione* and above, Fig. 16). *Navicula litoralis, N. Smithii, Nitzschia palea* var. *tenuirostris, N. bilobata, N. subtilis* and *N. lanceolata* var. *incrustans*. The prevalence of species of the genus *Nitzschia* amongst these forms restricted to the higher and firmer soil is noteworthy.

III. *Upper zones* (*Aster-Salicornia* and above, Fig. 19). *Navicula formosa, N. constricta, N. interrupta, Nitzschia obtusa* var. *scalpelliformis, N. intercedens* and *Navicula mutica*.

IV. *Lower zones* (*Aster-Salicornia* and lower, Fig. 20). *Navicula ammophila* var. *flanatica, N. Bombus, N. lanceolata* var. *phyllepta, Nitzschia Claussii* and *N. obtusa* var. *nana*.

V. *Marginal: Present all the year round* (Fig. 21). *Gyrosigma Wansbeckii, G. balticum, G. litorale, Nitzschia acuminata* and *Navicula spuria*.

More prominent during winter (Fig. 22). *Pleurosigma angulatum, Gyrosigma diaphanum, G. Fasciola, Nitzschia rigida, Navicula digito-radiata* var. *cyprinus, Surirella gemma* and *S. ovalis* var. *ovata*.

More prominent in summer (Figs. 23 and 24). *Scoliopleura tumida, S. latestriata, Amphora lineolata*[1], *A. proteus, Stauroneis Gregorii, Gyrosigma attenuatum* var. *scalprum* and *Nitzschia epithemioides*.

At Ynyslas zonation in the diatom flora does not seem to be nearly as pronounced. The lowest zones, open bare sand with *Salicornia* and the *Glyceria* zone rarely produce anything more than a few isolated specimens of *Scoliopleura tumida, Navicula cincta* var. *heufleri* or *Nitzschia rigida*. The upper

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[1] Sometimes abundant as high as the *Aster-Salicornia* zone.

zones, Armerietum, Lower Festucetum, and Juncetum usually supported examples of Groups I, II, and III above.

Kolbe (**32**) has recently published an ecological treatise on brackish diatoms. In this work he divides them into the following groups:

Euhalobic, forms which flourish best in water of the concentration of sea water.

Mesohalobic, forms which flourish in water less concentrated (0·5– 2 per cent.).

Oligohalobic, forms inhabiting water of less than 0·5 per cent. concentration. This group is further subdivided into:

Halophilous, fresh-water forms which are stimulated to increase their numbers in water slightly more saline than their customary water. These are often abundant in brackish water.

Indifferent forms, ordinarily fresh water, some of which, however, can exist in brackish water, although decreasing in number.

Halophobic forms, which find a very slight increase in the concentration of salts very detrimental.

Unfortunately Kolbe's work includes very few of the species commonly found on these two British salt marshes, so that detailed comparison is not very helpful. Mention may be made, however, of the striking absence of species of the two genera *Cymbella* and *Gomphonema* from the Dovey and Canvey salt marshes. Kolbe's work includes many representatives of these genera. The majority are described as "oligohalob," though there are a few species which are said to be "halophilous." On the whole, therefore, these diatoms do not favour strongly saline water.

CENTRICAE[1].

MELOSIRACEAE.

1. **Melosira Borreri** Grev.

Canvey. In pans, abundant with *Navicula crucigerum*, festooning grass roots and débris. r.

2. **M. Jurgensii** Ag.

Canvey. D. I–III.

3. **M. nummuloides** (Bory) Ag.

Canvey. D. I–III.

The last two species of *Melosira* have been previously recorded as brackish or marine, but they were only observed on the Canvey marsh in 1928 and are probably to be regarded as moisture-loving forms, rather than as true marsh diatoms. Following an extremely wet winter, both appeared in quantity with *Rhabdoderma minutum* in a wet ditch as bright brown festoons on dead grasses in water trickling over a temporary dam of débris. At first, in January,

[1] In this list, the order of the genera follows, as far as possible, that given in **West** and **Fritsch** (**50**).

M. Jurgensii was present in greater abundance, but when collections were made in March, *M. nummuloides* seemed to have increased in quantity. After this the marsh became drier as the spring advanced, the channel containing them drained, and both forms disappeared.

4. M. (Paralia) sulcata Ehr. f. radiata Grun. (*Orthosira marina* W. Sm.).

Canvey. All zones. Rare or occasional. All the year round.
Ynyslas. All zones. Rare or occasional. All the year round.

This is the commonest of all the centric diatoms, being noted on more than thirty occasions, from both marshes and at all times of the year. It was never present, however, in any abundance, occurring as isolated individuals or short filaments and it was always rare. Very often only occasional empty frustules were to be seen. On the whole, it is probable that this species is not a real marsh inhabitant, but, being a common and widely distributed marine diatom, it is frequently deposited by flooding tides on all parts of the marsh.

COSCINODISCACEAE.

5. Cyclotella Meneghiniana Kütz.

Canvey. B, C, and E. Rare, sporadic.

This diatom, which is common in fresh waters, is known, however, to be capable of accommodating itself to salinity and to occur in estuaries (see Peragallo (**39**), p. 435).

6. Coscinodiscus excentricus Ehr. in V. H., 1880, p. 217, t. 130, f. 8.

Canvey. C, rare. VII.

The individuals were about 47μ in diameter. Probably the species is more general than this one observation indicates, but it is very rare, and probably only such individuals as are washed up by the tide are to be found. It is not a true marsh form.

7. ? C. tabularis Grun. var. egregius (Rattray) Hustedt, 1928, p. 428, Fig. 230, on p. 427.

Canvey. A, and C. Rare.

This tiny diatom may possibly have been frequently overlooked, but it never occurred in any quantity. It is not restricted to any zone, and, like the preceding species, is probably deposited by receding tidal waters. The small frustules were only 12 or 13μ in diameter in the valve view, and frequently occurred in short filaments, as the girdle view showed. The areolations seemed to have no very definite order; they were 5–7 angled, and slightly larger in the centre, decreasing gradually towards the margins. The form is referred to this species with some hesitation, since the hyaline margin described by most authors was not visible in the valve view, though in the girdle view it could be made out quite distinctly that the areolations do not extend to the limits of

the valve. The valves are slightly concave or convex (possibly partly due to the collapsing of the frustules in preparation by burning), and this might quite well explain why the margins of the valve are not clearly visible in the valve view.

HELIOPELTACEAE.

8. **Actinoptychus undulatus** (Ehr.) Ralfs.

Canvey. All zones, rare. All seasons.
Ynyslas. B, C, and D. All zones, rare. All seasons.

This is a very general constituent, though never occurring in great numbers; it is one of the most frequent of the centric diatoms and is not restricted as regards level or season.

BIDDULPHIACEAE.

9. **Biddulphia Smithii** (Ralfs), V. H., 1880, p. 207, t. 105, f. 1, 2.

Canvey. A, and B. ii, xi.

10. **B. aurita** (Lyngb.) Bréb. in V. H., 1880, p. 205, t. 98, f. 4-9.

Canvey. All zones, rare. No seasonal periodicity indicated.

Though not observed at Ynyslas this form is occasional at Canvey, although it is rare as regards numbers.

PENNATAE.

TABELLARIACEAE.

11. **Rhabdonema minutum** Kütz. in V. H., 1880, p. 166, t. 54, f. 17-19.

Canvey. B. and D. i, viii.

This diatom appeared in great abundance in a ditch during the very wet winter of 1927-8. It was dominant in the ditch, and almost pure, species of *Melosira* being its only associates (see p. 172). During the wet season it was also present to some extent on the soil as well. Its occurrence is probably sporadic, since with the drier conditions of the advancing spring it disappeared.

RHAPHIONEIDACEAE.

12. **Rhaphioneis amphiceros** Ehr. formae.

Canvey. All zones. All seasons.

This was quite a frequent species on the Canvey marsh, though not occurring in great numbers. In form it was very variable, but the relatively wide frustules usually attributed to var. *rhombica* Grun. in Peragallo (**39**, t. 83, f. 21-23) were perhaps more common than the typical form. Forms approximating to f. 23 of Peragallo were particularly frequent. Its records show no restriction as regards level or season, but because of its small numbers it seems doubtful whether it multiplies on the marsh, being only an occasional form at the most.

13. R. belgica Grun. in Peragallo, 1897, p. 330, t. 83, f. 24–26.

Canvey. A. I.

This species was only observed on one occasion, when it was present as scattered individuals. Unless frequently overlooked on account of its resemblance to the preceding species it must be quite a rare constituent.

FRAGILARIACEAE.

14. Synedra barbatula Kütz., Peragallo, 1897, p. 316, t. 80, f. 5.

Ynyslas. A. VIII.

There is only one record for this species, but it may possibly be a more general constituent. It was epiphytic on drift *Enteromorpha* lying on the open mud at Ynyslas.

ACHNANTHACEAE.

15. Achnanthes brevipes Ag.

Canvey. A, B, C, and D. All seasons.
Ynyslas. A, B, C, D, and F. All seasons.

This species, which is known to be widely distributed in marine and brackish waters, occurred as an epiphyte. It was the usual and often the only epiphytic diatom which occurred on *Rhizoclonium* and *Enteromorpha* spp. Occasional frustules were found free. It never occurred in great quantity.

16. A. delicatula Kütz. in V. H., 1885, p. 130, t. 27, f. 3, 4.

Ynyslas. B, C, D, and F. III, VI.

This is a form which is known to be brackish and is recorded for the North Sea. It occurred only as a rare specimen amongst other diatoms between the higher plants.

NAVICULACEAE[1].

17. Navicula (Diploneis) constricta Grun.

Ynyslas. C, D, and F. All seasons. Fig. 19, 6.

This species was never found at Canvey. With two exceptions all the records for it are from the Junctetum, of which it seems to be a constant constituent. It probably has a preference for the higher and drier parts of the marsh. The striations were somewhat finer than usual, 12 in 10μ.

18. N. (Diploneis) interrupta Kütz.

Canvey. B, and E. XI.
Ynyslas. B, C, and D. I, VI. Fig. 19, 7.
L. 45–55μ; B. 15–17μ; B. constr. 6–10μ; striat. 10 in 10μ.

This is an occasional species, which, however, reached some degree of abundance on one or two occasions. There is some indication that it prefers the intermediate and higher portions of the marsh. It is widely distributed in

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[1] In the genus *Navicula* and other naviculoid diatoms, the species are listed for the most part in the order given by **Cleve (10)**.

brackish waters (cf. Kolbe (**32**), p. 115). Van Heurck (**49**) gives the striations as 4 in 10μ. The present examples agreed better with the figures given by Peragallo (**39**, p. 114).
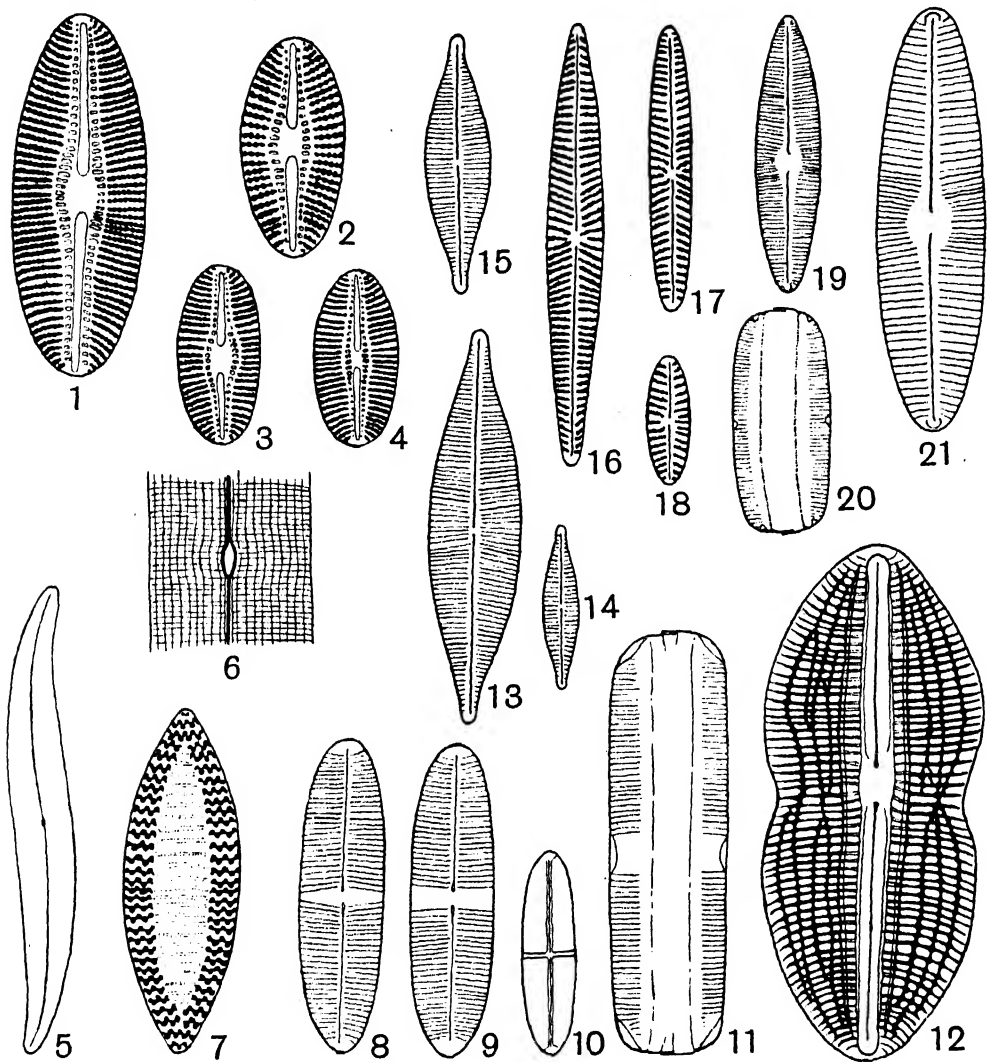
FIG. 15. Salt marsh diatoms not restricted to any particular level. *1–4, Navicula vacillans* A. S.; *3, 4,* upper and lower valves of the same individual; *5, 6, Gyrosigma Spenceri* W. Sm.; *7, Nitzschia navicularis* Bréb.; *8–11, Stauroneis septentrionalis* Grun.; *8, 9,* upper and lower valves of the same individual; *12, Navicula didyma* Ehr.; *13–15, N. gregaria* Donk.; *16, N. cincta* Ehr.; *17, 18, N. cincta* var. *heufleri* Grun.; *19–21, N. subinflata* Grun. var. *elliptica* Cl. *6, 8, 9, 11,* and *21,* × 1935; all others, × 963.

19. N. (Diploneis) didyma Ehr.

Canvey. All zones. All seasons.
Ynyslas. All zones. All seasons.   Fig. 15, *12.*

This is a very frequent species, though rarely found in great abundance. It is usually represented only by an odd specimen or so, but was once found in

great abundance in the plankton of a pan full of standing water at Canvey in June, and also in the same month amongst *Rhizoclonium* at the margin of a large channel at Ynyslas. Possibly it prefers the moister habitats, but the records are not very conclusive on this point.

20. **N. (Diploneis) Bombus** Ehr. in Cleve, 1894, p. 90; Peragallo, 1897, p. 119, t. 18, f. 10, 11.

Canvey. A, and B. No seasonal variation indicated.
Ynyslas. In pan. Fig. 20, *5*.

This is not a common form, having been observed only on four occa ions, and never in great quantity. On two occasions it was found in a pan of standing water, and it probably prefers the moister habitats. The specimens were sometimes well under the size usually given for this species, varying from 26 to 45μ in length.

21. **N. (Diploneis) ovalis** Hilse (*N. elliptica* Kütz.).

Canvey. C, D, and E. No seasonal periodicity indicated.
Ynyslas. D, and F. Fig. 16, *8*.

This is a typical fresh-water species. There is a var. *grandis* mentioned by Cleve (**10**) which is fossil and brackish, but the present individuals do not seem to agree with this. There is a definite indication in the records for this species on the two marshes that it prefers the upper zones, where it is a not uncommon constituent of the diatom flora. At Canvey it is quite frequent in the *Glyceria* zone, and similarly at Ynyslas it is common in the Juncetum, being rarely found at lower levels on either marsh. A typical fresh-water species, it is not surprising that on the salt marsh it only occurs where submergence by the sea is infrequent. Kolbe (**32**), refers to it as "indifferent" (see p. 172).

22. **N. (Diploneis) litoralis** Donk. in Cleve, i, 1894, p. 94 (var. *subtilis* in Peragallo, 1897, p. 126, t. 20, f. 11).

Canvey. B, C, D, and E. No periodicity indicated.
Ynyslas. B, C, D, and F. Fig. 16, *5-7*.
L. 22–30μ; B. 10 13μ; striae 14–18 in 10μ.

This was a very common species. The specimens were rather small and finely striate as compared with the descriptions of Cleve and Peragallo. A preference for the higher ground is indicated, since the species was only found on one occasion lower than the *Obione* zone at Canvey, and at Ynyslas it was found in the greatest abundance in the Juncetum zone, though it occurred in all zones except the open sand. The specimens often seemed to be transitional to the next (*vide infra*).

23. **N. (Diploneis) vacillans** A. S. in Peragallo, 1897, p. 126, t. 20, f. 15.

Canvey. All zones. All seasons. Fig. 15, *1-4*.
L. 35–52μ; B. 14–17μ; striae 10–12 in 10μ.

This species seems, on the whole, to prefer the softer mud of the lower zones. It is a common form on the Canvey marsh but was not observed at

Ynyslas. At Canvey, although rarely occurring in quantity on the open mud, it was a frequent constituent of any zone between the margin and the *Obione* zone. It was found in abundance very occasionally in the Upper *Glyceria* zone, but when this happened it could usually be ascertained that a high tide had taken place not long before the samples were collected. This might account for the specimens being washed up above their normal level on the marsh. It is probably not a normal constituent of the *Glyceria* zone at Canvey.
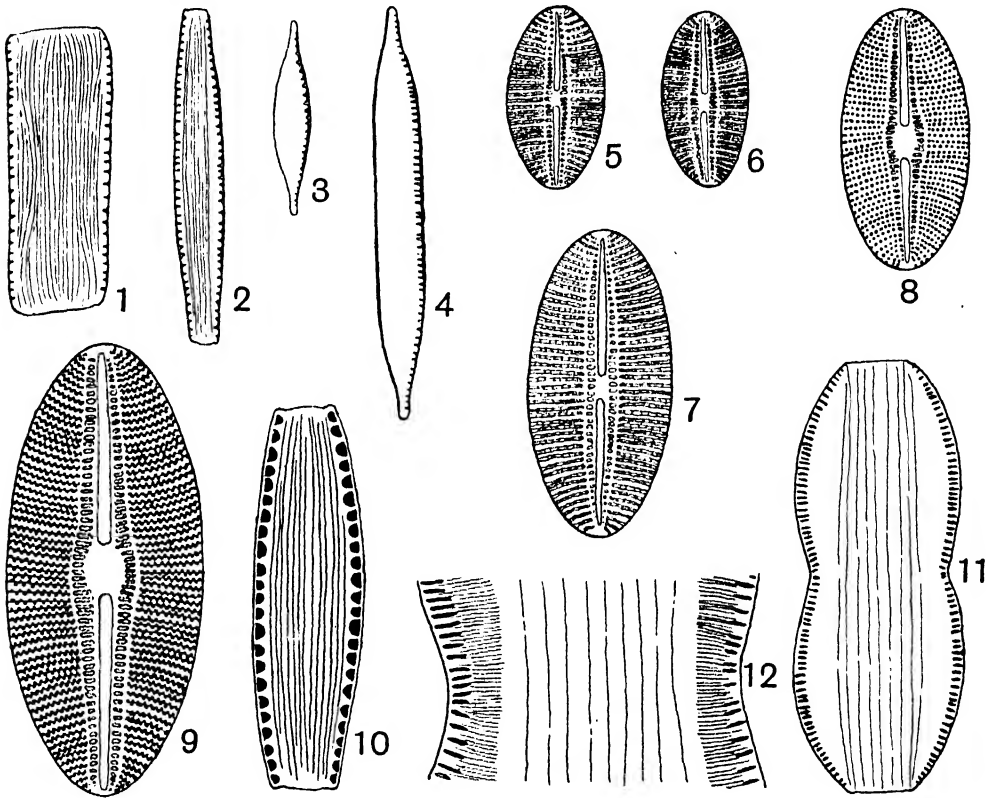
Fig. 16. Diatoms found chiefly in the top zones of the marsh (*Obione* and *Glyceria* zones at Canvey). *1–3, Nitzschia subtilis* Kütz.; *4, N. palea* (Kütz.) W. Sm. var. *tenuirostris* V. H.; *5–7, Navicula litoralis* Donk.; *8, N. ovalis* Hilse; *9, N. Smithii* Bréb.; *10, Nitzschia lanceolata* W. Sm. var. *incrustans* Grun.; *11, 12, N. bilobata* W. Sm. *11*, × 552; all others, × 963.

The three preceding species, *N. elliptica, N. litoralis* and *N. vacillans* are not readily distinguished from one another, the last two being exceedingly difficult to separate. *N. elliptica* can be recognised by its rather larger size and by the distinctly punctate nature of its striae. The punctae are large, distinct and widely separated from each other (Fig. 16, *8*). It is quite a different matter as regards the other two species, in neither of which are the striae so readily resolved into punctae. It is rather questionable whether the last two are specifically distinct. At any rate, individuals were observed from the *Aster* zone at Canvey in which the one valve had the characters of *N. vacillans*,

and the other of *N. litoralis* (Fig. 15, *3*, *4*). In its typical form, *N. vacillans* seems to have its striae a little coarser than *N. litoralis*, i.e. about 10–12 in 10μ, and the two conspicuous furrows on either side of the median line bulge somewhat round the central nodule to enclose a lanceolate space (Fig. 17, *1*, *2*). *N. litoralis* has striae measuring about 18 in 10μ, and its furrows are parallel for their whole length, enclosing a rectangular rather than a lanceolate space around the central nodule (Fig. 16, *5–7*). In transitional forms found at Canvey the striae were usually 12 or 13 in 10μ, whilst the area around the central nodule tended to be lanceolate rather than rectangular, and the two valves of the same individual sometimes varied in the last character. In spite of these difficult cases, the extremes of structure typical of the two species are remarkably distinct, although as Cleve says (**10**, I, p. 7), many of these species are connected by intermediate varieties, and because of this it seems doubtful whether these two should have specific rank. Ecologically, however, they seem to be distinct. *N. vacillans* has not been observed at Ynyslas, and at Canvey *N. litoralis* rarely descends into the *Aster-Salicornia* or marginal zones, which are quite typical habitats for *N. vacillans*. It would seem that *N. vacillans* has, on the whole, a lower location on the marsh than *N. litoralis*, although they overlap for part of their area.

24. N. (Diploneis) Smithii Bréb.

Canvey. All zones. All seasons.
Ynyslas. B, C, D, and F. All seasons. Fig. 16, *9*.
L. 56–85μ; B. 25–35μ; striae 8–10 in 10μ.

This species is readily distinguished from the preceding three by its larger size and its striae composed of double rows of minute punctae. It is undoubtedly associated more particularly with the higher zones of the marsh, occurring very abundantly in the *Glyceria* zone at Canvey and the Juncetum at Ynyslas. When observed on the lower levels of the marsh, as on one occasion in the marginal zone at Canvey and the Glycerietum at Ynyslas, it was exceedingly rare. It was also a rare constituent of the plankton flora of pans at Canvey. It reached its highest development on the Juncetum at Ynyslas.

25. N. blanda A. S. in Cleve, 1894, I, p. 62; Peragallo, 1897, p. 77, t. 14, f. 2, 3.

Canvey. Plankton of pan. VI.
L. 46–57μ; B. about 12μ; striae 7 in 10μ.

This species was only observed on one occasion, when it was present in some abundance amongst other diatoms in standing water. It is possibly not a regular constituent of the marsh flora proper, but was probably induced to multiply and become abundant by the warmth and undisturbed conditions in the pan.

26. N. pygmaea Kütz.

Canvey. All zones. All the year round.
Ynyslas. All zones. All the year round. Fig. 21, *1*.

This is one of the most frequent forms on both marshes. It enjoys a very wide distribution in all zones, and may be very common at any level. Perhaps

it reaches its greatest development, however, in the marginal mud at Canvey, where it was very abundant July–November. On one occasion in June it was very frequent in the plankton of a pan. At Ynyslas it was never present in such great abundance, but was likely to occur at any level. Sometimes forms with slightly rostrate apices were present along with the typical form. Although observed at most times of the year there is some indication at Canvey that it is more abundant in summer. At Ynyslas it was not uncommon in March and June. Kolbe (**32**) describes this species as mesohalobic (see p. 172).

27. **N. gregaria** Donk.

Canvey. All zones. All seasons.
Ynyslas. All zones. All seasons.   Fig. 15, *13–15*.
L. 21–68 μ; B. 4·5–12 μ; striae parallel, 15–20 in 10 μ.

This is a species which approaches *N. cryptocephala*, from which it differs in its very narrow and almost negligible central area, and in its striae parallel for their whole length. In size it was exceedingly variable; once, when occurring in plankton, its dimensions were as much as double the normal, reaching 68 × 12 μ. The form of the frustule is likewise apt to vary somewhat, the apex being sometimes very definitely rostrate, and sometimes scarcely rostrate at all. This delicate little diatom is one of the most generally distributed on the two marshes. It occurs at all levels in both localities, and is a common constituent of the plankton of pans, enjoying an aquatic habitat equally with the drier conditions of the *Glyceria* zone at Canvey or the Juncetum at Ynyslas. After the unusual tides in November, 1927, at Ynyslas, this diatom was a common constituent of the line of débris surrounding full pans after the water had gradually receded (see Carter (**9**), p. 370). There was some indication that, though it has been found all the year round, it is most abundant June–September.

28. **N. crucigera** (W. Sm.) Cleve (*Schizonema cruciger* W. Sm.).

Canvey. In pan, epiphytic on submerged grass. I.   Fig. 17, *4–6*.
L. about 116 μ; B. about 11 μ; trans. striat. 18 in 10 μ.

The figures and descriptions of this species are not very satisfactory. Cleve (**10**, I, p. 111) gives the transverse striation as 12 in 10 μ and Van Heurck (**49**, p. 110, t. 16, f. 1) as 24 in 10 μ. In the present specimens it was intermediate between these figures, and the longitudinal striation was rather finer and more difficult to see. The figures of Van Heurck do not show the stauros properly, although the description of its being covered by two striae stouter than the rest agrees very well with the present specimens. The stauros is seen as a glistening bar. The specimens were in wide unbranched tubes, four or five abreast, and when examined in the living condition the frustules were actively motile, both those contained within the tube and those which had escaped. The species was seen only on one occasion.

29. **N. mutica** Kütz. forma *Cohnii* Hilse.

Canvey. B, and E. I, VII. Fig. 19, *4*.

This tiny diatom has only been observed on a few occasions at Canvey although there would seem to be habitats equally suitable at Ynyslas. On two occasions it was quite abundant in July in the *Glyceria* zone, which seems to be its natural habitat, for it was only found once below this level.

30. **N. subinflata** Grun. var. **elliptica** Cleve, I, 1894, p. 141; Peragallo, 1897, p. 61, t. 7, f. 44.

Canvey. All zones. Abundant. VII–IX.
Ynyslas. B, C, D, and F. III, VI, VII. Fig. 15, *19 21*.

This small species was slightly more slender than Cleve's dimensions, measuring about $30 \times 7\mu$, whilst Cleve gives $35 \times 13\mu$. Owing to difficulty in obtaining valve views, the identification of this species was not easy, and I am indebted to Mr David McCall of Dundee for valuable help in determining it. The striation of the valves is very delicate, 20–22 in 10μ, and the striae are parallel the whole length of the valve. There is a small lanceolate area surrounding the central nodule. In the girdle view two longitudinal series of minute dots can be distinguished. The diatom is often very abundant and has a very wide vertical range on both marshes, having been observed in almost every zone, although in general it is more abundant in the *Obione* and *Glyceria* zones at Canvey than in the lower zones. At Ynyslas it is also more abundant in the highest zones (Armerietum and above). The records seem to indicate that it is more commonly present in summer. It has not been seen at all in the winter months.

31. **N. scopulorum** Bréb. (*N. Johnsonii* Van Heurck).

Canvey. Colonising sod of *Obione* zone which had fallen into the channel 8 or 10 ft. beneath.
III, IV. Fig. 17, *1–3*.
L. $60–106\mu$; B. $10–20\mu$; trans. striat. 20–24 in 10μ.

This beautiful diatom was only observed in the one habitat. A solid lump of soil, loosened by erosion, had fallen into the soft mud of the channel and remained recognisable for some months before being disintegrated; it was abundantly covered with this diatom. *N. scopulorum* is very delicate and only slightly silicified. The preparations were not made by cleaning with acid, but by incineration on the slide. Even so, the delicate frustules buckled and twisted, so that relatively few retained their characteristic form. The striae are exceedingly delicate, and can be resolved into minute punctae. They are parallel throughout their whole length, and measure 20–24 in 10μ. In the middle line the striae nearly extend to the raphe, except for a short length around the central nodule. In the valve view it is seen that the central and end nodules are all rather elongated, a feature which has not hitherto been emphasised. The girdle is complex, showing at least four longitudinal lines.
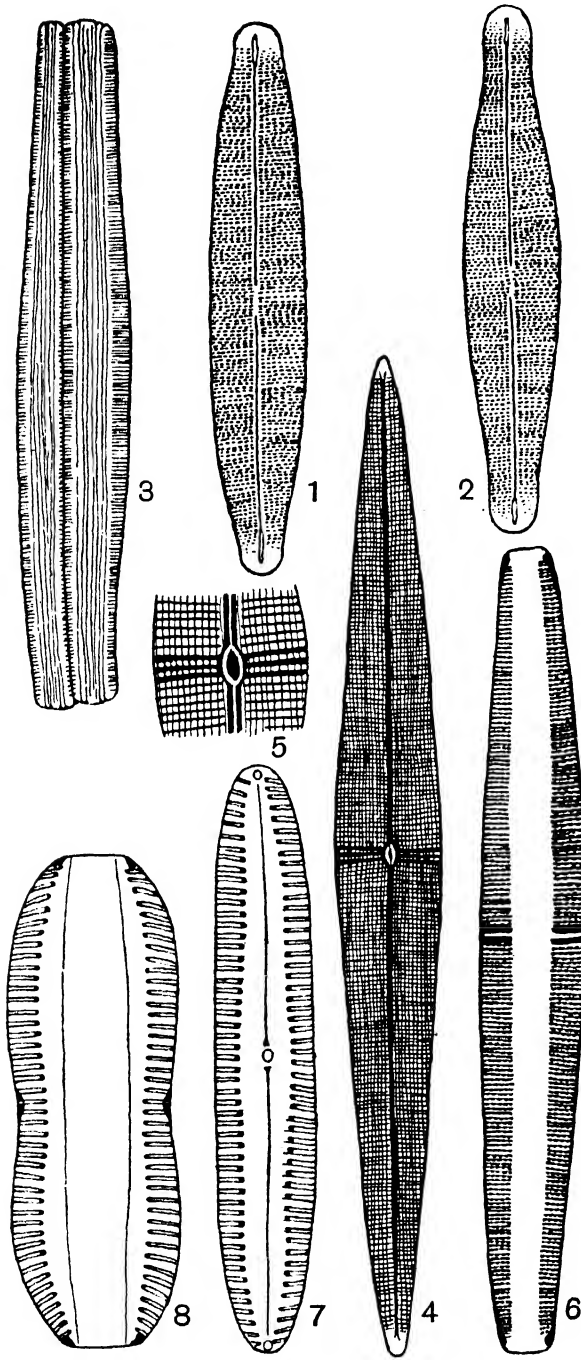
FIG. 17. Diatoms of sporadic occurrence. *1–3, Navicula scopulorum* Bréb.; *4–6, N. crucigera* (W. Sm.) Cleve; *7, 8, N. hemiptera* Cl. *5,* × 2150; all others, × 1070.

32. N. Grevillii Ag.

Canvey. All zones. All seasons.
Ynyslas. All zones. All seasons.
L. about 20 μ; B. about 5·5 μ; striat. 18 in 10 μ.

Fig. 18, *3–5.*

This is a form which may occur in all zones not frequently disturbed by tidal action. Whenever silting up is in progress, and the level of the soil is raised so that it is not frequently submerged, this is one of the first plants to appear.

At Canvey, silting often results in the formation of small rounded hummocks a foot or two in diameter which lie like islands out in the channel (see Carter (9), p. 366). Long before phanerogams have established themselves on this higher ground, *N. Grevillii* will be represented, along with Cyanophyceae and *Vaucheria*. At higher levels in the marsh also, as observed at Canvey, erosion may denude the surface of the soil of its existing algal vegetation (largely *Enteromorpha* and *Vaucheria*). As soon as erosion ceases *Navicula Grevillii* is the first to establish itself. Its habit of growth, the frustules being contained in tough gelatinous tubes, renders it of the greatest importance as a first coloniser. The tubes are firmly lodged between the small particles of soil and it is very difficult to free them from adhering mud. Thus its tubes form a firm brown covering over the surface of the soil, which must be of great importance in preventing the further washing away of the surface by the action of the tides. *N. Grevillii* is often found in quantity on the surface of the soil in any zone above the *Aster-Salicornia* level, especially if there is a brown coloration and no apparent algal covering. Such apparently bare soil often possesses a firm outer layer in which the tubes of *N. Grevillii* ramify.

At Ynyslas the more compact nature of the turf formed by the grasses and other phanerogams prevents *N. Grevillii* from playing such an important rôle. Here it has more scope for development in the Juncetum, where there are extensive stretches of bare soil free from phanerogams and larger algae, and perhaps it is even more important on the vertical surfaces of the marginal escarpments. Experiment proved that *N. Grevillii* is the first coloniser on bared soil in this region (see Carter (9), p. 366). Furthermore the alga is present at all times of the year, so that this fact also makes it more important as a protector of bare soil.

Its frustules were very tiny, smaller than the dimensions usually given. Its nodules and striation are very delicate and only seen with difficulty. The end nodules are some distance from the ends of the valves and the girdle view is complex. As a rule the frustules are in single file in the tubes.

33. N. Bulnheimii Grun. var. belgica Cleve.

Canvey. B, C, and E. VII, VIII.
Ynyslas. C. VI.
L. 33–41 μ; B. 6–7 μ; striat. 28 in 10 μ.

Fig. 18, *6–8.*

This form was found on several occasions. It may inhabit any soil which appears to be bare and not undergoing erosion, but it has not been seen below the *Aster-Salicornia* zone at Canvey. Its frustules are usually crowded in tubes, several abreast, but they are sometimes free. The end nodules are

very distant from the ends of the frustule, and the striae, which are exceedingly
fine, are slightly more distant in the centre of the valve and also leave a small
rounded area around the central nodule. The girdle view resembles greatly that
of *N. Grevillii*.
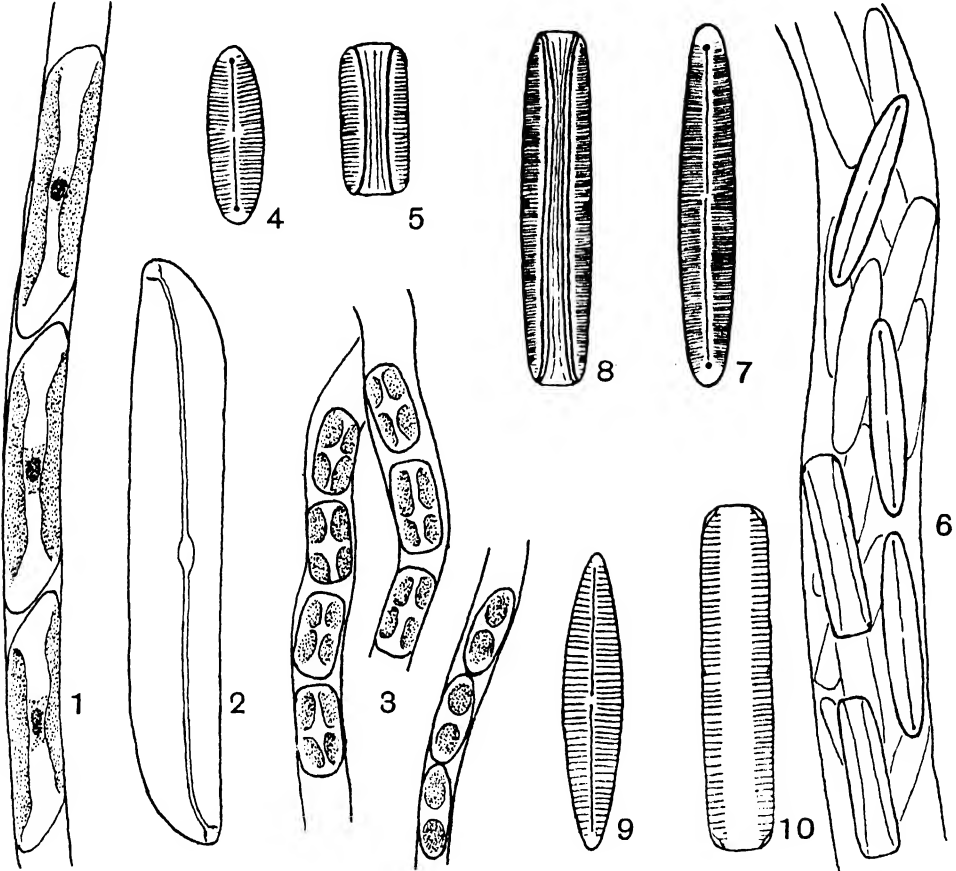
FIG. 18. Filamentous diatoms. *1, 2, Gyrosigma scalproides* Rabenh. var. *eximia* Thw.; *3–5,*
Navicula Grevillii Ag.; *6–8, N. Bulnheimii* Grun. var. *belgica* Cl.; *9, 10, N. ramosissima* Ag.
1, 3 and *6,* × 613; all others, × 1070.

34. **N. viridula** Kütz.

Canvey. All zones. No seasonal periodicity.

This species, which was only found at Canvey, was very rare, occurring
only as very isolated individuals. Kolbe **(32)** describes it as "oligohalob."
This is scarcely in accordance with its occurrence at the margins of the marsh,
but since it was always so rare, its requirements are not easily defined.

35. **N. cincta** Ehr.

Canvey. Plankton of pan. Rare.. VI.
Ynyslas. C. Rare. IX.   Fig. 15, *16.*

This species was only noted on two occasions, but possibly it was at times
confused with its var. *heufleri*, which is far more common. When observed at

Ynyslas it was in a scum left by the receding water of pans which had been filled to overflowing by unusually high tides (see Carter (9), p. 370). All three forms were unusually large in this peculiar habitat, suggesting that the conditions for diatom growth were particularly favourable.

var. **heufleri** Grun.

Canvey. All zones. All seasons.
Ynyslas. All zones. All seasons. Fig. 15, *17, 18.*

This tiny diatom is one of the most frequent of all Naviculas, and was equally abundant on both marshes. Although not uncommon in the marginal regions it becomes more important at higher levels, where it often becomes dominant owing to the falling out of species more dependent on moist conditions. It was very variable in size and sometimes seemed to grade into the type form.

36. **N. peregrina** Ehr.

Ynyslas. B, C, D, and F. No seasonal periodicity indicated. Fig. 19, *1.*
L. 90 μ; B. 19 μ; striae 8 in 10 μ.

This species, occurring at Ynyslas only, seems to have a preference for the higher levels of the marsh. In the lower levels (Glycerietum) it only occurred as a very rare constituent. Once it was found in mud at the bottom of a full pan, but then also was rare. In the Lower Festucetum and Juncetum it was sometimes present in fair quantity.

37. **N. digito–radiata** Greg. var. **Cyprinus** (Ehr.) W. Sm.

Canvey. A, B, and D. All seasons.
Ynyslas. B, C, D, and F. Fig. 22, *7.*

This is a species whose natural habitat seems to be in the lower parts of the marsh, where it sometimes occurs in abundance. It is especially common in the marginal zone at Canvey, where it may become locally dominant especially in the winter months. It is always rare at any level higher than zone A. On one occasion it was not uncommon in the plankton of a pan. At Ynyslas the conditions for the development of this species are apparently not realised to the full, for although observed on several occasions, it occurred only as an occasional individual. At Canvey there was a definite indication that this species has a winter maximum, since it is to be found at the margins of the marsh from November to February in great quantity. Between July and October it was always rare. Peculiarly enough the Ynyslas records are all in the months of June and July, but, as already pointed out, it was only an occasional species on this marsh.

38. **N. lanceolata** Kütz. var. **phyllepta** (Kütz.) Cleve in V. H., 1885, p. 88, t. 8, f. 40.

Canvey. B. VII, IX.
Ynyslas. Amongst *Rhizoclonium* in large channel. Fig. 20, *1.*
L. 33 μ; B. 8 μ; striae 17 in 10 μ.

This species was observed only on four occasions, but possibly, since it was rare, it may sometimes have been overlooked. It was usually found in the *Aster-Salicornia* zone at Canvey, indicating a preference for soil moist, but not

frequently disturbed by tides. Usually it occurred as isolated specimens amongst *Navicula subinflata* var. *elliptica* and *Amphora lineolata*. A peculiar feature which seemed to be fairly constant is the fact that the striae seem to be more strongly radiate on one side of the valve than on the other. This feature is slightly indicated in Van Heurck's figure, although there is no reference to it in the text.

39. **N. ammophila** Grun. var. **flanatica** Grun.
Canvey. A, B, and D. No seasonal periodicity indicated.
Ynyslas. B, and C.   Fig. 20, *2*.
L. about 40 μ; B. about 8 μ; striae 12 in 10 μ.

This species is one which has never been found on the higher levels of the marsh. It is possibly frequently overlooked, as only isolated specimens occur.

40. **N. ramossissima** Ag. (*Schizonema ramossissima* Ag.).
Canvey. B. Also in pan with *Melosira*. I, VI.   Fig. 18, *9, 10*.

This species was only observed on two occasions, but may perhaps have been overlooked. In both cases it was present in some abundance. The specimens found in a pan in January, 1930, had their striae slightly radiate and seemed to approximate to the var. *setaceum* in V. H. (**49**, p. 111, t. 15, f. 13).

41. **N. spuria** Cleve in Peragallo, 1897, p. 92, t. 12, f. 5.
Canvey. A, and B. No seasonal variation indicated.
Ynyslas. B, and C. No seasonal variation indicated.   Fig. 21, *5*.
L. about 74 μ; B. about 12 μ; striae 8 or 9 in 10 μ.

This seems to be a somewhat uncommon species. It never occurs in quantity and seems to be restricted to the marginal zone. At Canvey it was only once found at a higher level than the *Aster-Salicornia* zone, when, at the time of a spring tide, it occurred in the *Glyceria* zone; possibly it was deposited there by the receding tidal water. At Ynyslas it was only observed as a rare specimen on two occasions. This species is known from the Mediterranean region, but so far as I know it is a new record for this country.

42. **N. humerosa** Bréb. in Peragallo, 1897, p. 146, t. 27, f. 20.
Canvey. A. No seasonal periodicity indicated.
Ynyslas. A, and F. No seasonal periodicity indicated.
L. about 47 μ; B. about 23 μ; striae 10 in 10 μ.

This form, observed on five occasions, is always very rare.

43. **N. Baileyana** A. S. in Peragallo, 1897, p. 148, t. 27, f. 12, 13.
Ynyslas. In channel and in full pan. VI, VII.

This is a very rare species, only observed on two occasions, in a rather moist situation.

44. **N. abrupta** Greg. in Peragallo, 1897, p. 132, t. 21, f. 35–37.
Canvey. B. VII.
Ynyslas. B, C, D, and F. VI. .

Although this species was observed on several occasions, it was always very rare. It seems to prefer the higher zones of the marsh, and the summer months of the year.

45. **N. formosa** Greg. in Cleve, I, 1894, p. 57 (*N. Liburnica* Grun. in V. H., 1880, p. 102, t. 11, f. 3).

Canvey. B, C, and E. III–IX.

Ynyslas. B, C, D, and F. I–VII. Fig. 19, *2, 3*.

L. about 80 μ; B. about 18 μ; striae about 13 or 14 in 10 μ.

This form is very common at certain times of the year. It is most abundant in the *Aster-Salicornia* zone at Canvey, where it is often dominant and some-
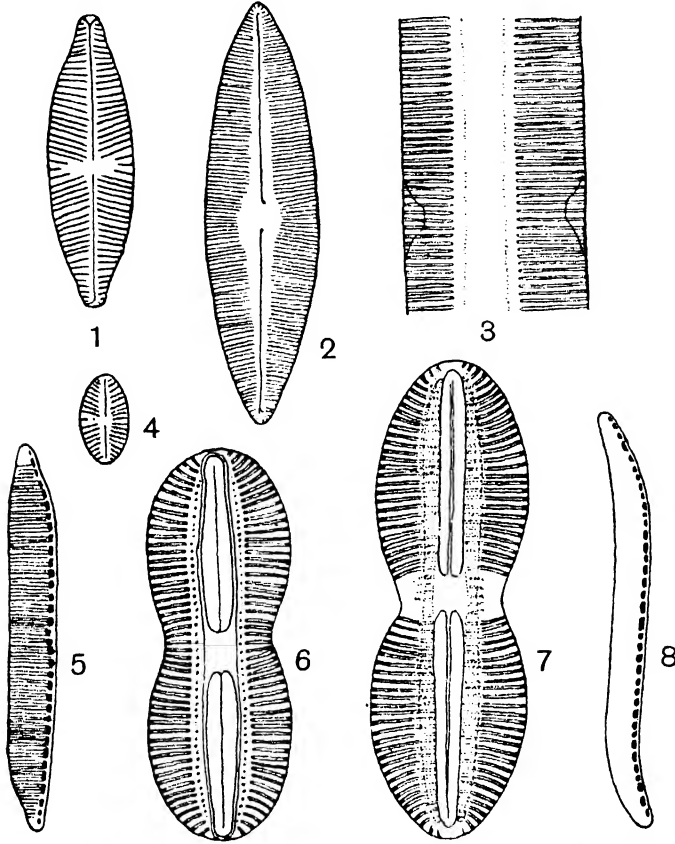
FIG. 19. Diatoms found in the upper zones of the salt marsh (*Aster-Salicornia* zone and zones higher). *1, Navicula peregrina* Ehr.; *2, 3, N. formosa* Greg.; *4, N. mutica* Kütz.; *5, Nitzschia obtusa* W. Sm. var. *scalpelliformis* Grun.; *6, Navicula constricta* Grun.; *7, N. interrupta* Kütz.; *8, Nitzschia intercedens* Grun. *1* and *2*, × 613; all others, × 1070.

times pure. It was never found at a lower level than the *Aster-Salicornia* zone, although it was often present in less quantity at higher levels. It was also found at the margins of the dry muddy bottom of an empty pan.

At Ynyslas it was never found in such great quantity, and here also it was rarely present below the *Armeria* zone.

This is one of the forms with a spring and summer maximum. It was almost entirely absent from October to February, both at Canvey and Ynyslas. In March it became very abundant at Canvey in the *Aster-Salicornia* zone, remaining so until September.

Some difficulty was experienced with the identification of this species, owing to the longitudinal lines being invisible. I am very greatly indebted to Mr McCall of Dundee for referring it to this species.

46. **N. hemiptera** Cleve, II, 1894, p. 85.

Canvey. A (local). IX.　　　　　　　　　　　　　　　　　　　　Fig. 17, *7, 8*.
L. about 57–68 μ; B. about 11 μ; striae 8 or 9 in 10 μ.

This species was only observed on one occasion, when it occurred in some quantity as local brown patches on the marginal mud with *N. pygmaea* and *N. cincta* var. *heufleri*. As far as I know it has not previously been recorded for a marine habitat. According to Kolbe (**32**), it prefers less than 0·5 per cent. of salt, which is peculiar in view of its occurrence at the margins of the Canvey marsh.

47. **Scoliopleura tumida** (Bréb.) Rabenh.

Canvey. A, B, and C. All the year round.
Ynyslas. A, and C. All the year round.　　　　　　　　　　　Fig. 24, *5–7*.
L. about 100 μ; B. about 22 μ; striae 13 or 14 in 10 μ.

This is a form which prefers the lower zones of the marsh, being only once observed above the *Aster-Salicornia* zone at Canvey and only once above the Armerietum at Ynyslas. Like *Navicula formosa*, it has a decided spring and summer maximum, being usually very abundant from March to September. In the winter months it does not disappear so completely as *Navicula formosa*, and may persist in very slight quantity, especially on the marginal mud. It has been found in the dry mud at the margins of a pan at Canvey, and also in the plankton of a full pan.

Superficially this species shows some resemblance to *N. formosa*, from which it is readily distinguished however by its twisted frustules and the more definitely punctate nature of its striations. The two species differ in their distribution on the marsh, *N. formosa* preferring the *Aster-Salicornia* and higher zones, and *Scoliopleura*, the *Aster-Salicornia* and lower zones. In the *Aster-Salicornia* zone they are often very common together.

48. **S. latestriata** (Bréb.) Grun.

Canvey. A. No seasonal variation indicated.　　　　　　　　　Fig. 24, *3, 4*.

This species was usually exceedingly rare and very restricted in its distribution on the marsh. Its usual position is in the moist marginal mud, and it was once observed in the plankton of a pan.

49. **Stauroneis septentrionalis** Grun. in Cleve, I, 1894, p. 146.

Canvey. A, B, C, and E. VI–IX.
Ynyslas. C, D, and F. I, III, VI.　　　　　　　　　　　　　　Fig. 15, *8–11*.
L. 20–28 μ; B. 5–6 μ; striae 30 in 10 μ.

The specimens were usually more finely striate than normal, since Cleve gives 23 in 10 μ. The form of the frustule, with its nearly parallel sides, approximated somewhat to the figure of *S. salina* in Peragallo (**39**, t. 7, f. 22), but the

stauros is different, and the striation is much finer. The width of the stauros varies, even in the two valves of the same individual (cf. Fig. 15, *8, 9*), being sometimes very narrow and sometimes quite broad.

This form is obviously characteristic of the upper zones, never being found below the Armerietum zone at Ynyslas, and only once below the *Aster-Salicornia* zone at Canvey. It is a feature of the *Obione* and *Glyceria* zones at Canvey, and the Juncetum zone at Ynyslas. At Canvey it appeared to be a late summer form, but at Ynyslas this was not apparent.
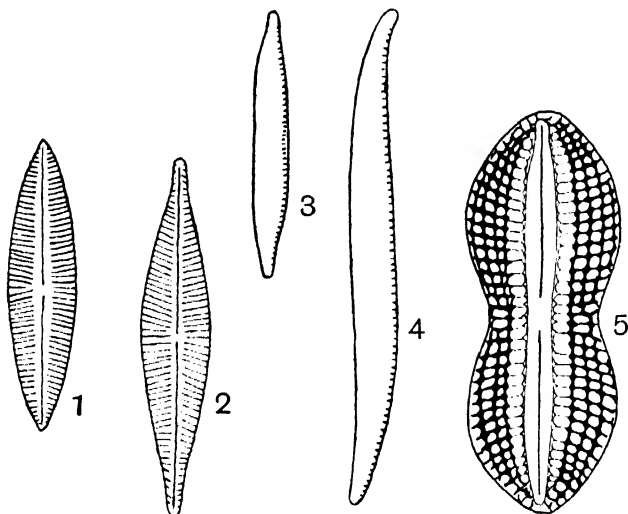
FIG. 20. Diatoms common in the lower zones of the salt marsh (*Aster-Salicornia* zone and lower). *1, Navicula lanceolata* Kütz. var. *phyllepta* (Kutz.) Cleve; *2, N. ammophila* Grun. var. *flanatica* Grun.; *3, Nitzschia obtusa* W. Sm. var. *nana* Grun.; *4, N. Claussii* Hantzsch; *5, Navicula Bombus* Ehr. All × 1070.

50. **S. Gregorii** Ralfs in Peragallo, 1897, p. 56, t. 7, f. 25, 26.

Canvey. A. Also in plankton of a pan. No seasonal variation.   Fig. 24, *1, 2*.
L. 38–100 μ; B. 7·5–17 μ; striat. 20 in 10 μ.

The species is never represented by a large number of individuals, but is not infrequently encountered in the marginal regions, indicating a preference for the moister habitats.

51. **Pleurosigma angulatum** Queck.   Fig. 22, *3, 4*.

var. **quadratum** (W. Sm.) Peragallo.

Canvey. A, and B. XI–III.
Ynyslas. In débris around pan. XI.   Fig. 22, *5, 6*.

This species, like *Gyrosigma balticum* and *Surirella gemma*, is restricted almost entirely to the open stretches of bare mud, being rarely found even as high as the *Aster-Salicornia* zone. It is very abundant at the margins of the marsh at Canvey, where it often forms, with *S. gemma*, a distinctly visible brown film, extending also into the floors of all the smaller channels. It reaches

its highest development in November–March, and is very rare in the summer months. It has also been found in the plankton of a pan. It is one of the most conspicuous forms at Canvey, where it occurs in several forms, some individuals being typical in size and form, $240 \times 50\mu$, whilst others agree with var. *quadratum* in their relatively wider frustules, $190 \times 50\mu$. Very often in the marginal mud, considerably smaller individuals of the *quadratum* type occurred among the larger individuals. These small specimens were only half the size of the more numerous large ones, measuring about $95 \times 28\mu$ (Fig. 22, *6*). There were no intermediate specimens between the large and small forms. The striation of the type form and the small quadrate form is about 22 in 10μ, of the large quadrate form, 18 in 10μ.

At Ynyslas the species was only observed once, occurring with *Gyrosigma Spenceri* and other forms in some quantity in a scum left around each pan as a result of overflowing after an unusually high tide (November, 1927, cf. Carter (**9**), p. 370).

52. **Gyrosigma diaphanum** in Cleve, I, 1894, p. 115, II, t. 1, f. 6.

Canvey. A, B, and D. XI–III, rare in VIII, IX.
Ynyslas. Bottom of pan and in channel. VII.   Fig. 22, *1, 2*.
L. about 100μ; B. about 20μ; trans. striat. 30 in 10μ.

This is another species which prefers the soft mud of the lowest zones. At Canvey it was rarely found higher than the marginal region, and at Ynyslas, where it was much rarer, it was only found on bare mud. On the Thames marsh it sometimes became very abundant, especially in the winter months; in the summer it was not so frequently found. The striation of this species is very fine and not easy to see. The longitudinal striae are even finer than the transverse.

53. **G. attenuatum** Kütz. var. **scalprum** Gail. and Turp.

Canvey. A, B, and D. All the year round, but rare IX–III, common VII, VIII.
Ynyslas. Bottom of pan. VII.   Fig. 24, *8, 9*.
L. 125–160μ; B. 20–22μ; trans. striat. 20 in 10μ; long. striat. 17 in 10μ.

This species has a decided preference for the lowest zones and the moister habitats, being rare even in the *Aster-Glyceria* zone, though very common in the marginal and *Aster-Salicornia* zones, especially in the summer months.

54. **G. litorale** W. Sm.

Canvey. A, B, C, and D. All the year round, but commoner IX–III.
Ynyslas. In channel. VII.   Fig. 21, *6, 7*.
L. about 115μ; B. about 23μ; long. striat. 8 in 10μ; trans. striat. 18 or 19 in 10μ.

This is a species inhabiting the marginal mud more particularly, being rare in the *Aster-Salicornia* and higher zones, though it may become frequent in the moister parts of the *Aster-Glyceria* zone. It never reached the abundance of some of the other species of *Gyrosigma*, however, although it was very frequent in winter. In summer it was always rare.

55. G. Fasciola Ehr. (*Pleurosigma Fasciola* W. Sm.).

Canvey. A. I–III.

L. about 110 μ; B. about 15 μ; long. striat. 20 in 10 μ; trans. striat. 22 in 10 μ.

Fig. 22, *9, 10.*

This is not a common form and is only found as rare individuals in the winter months, in the diatom film on the marginal mud.
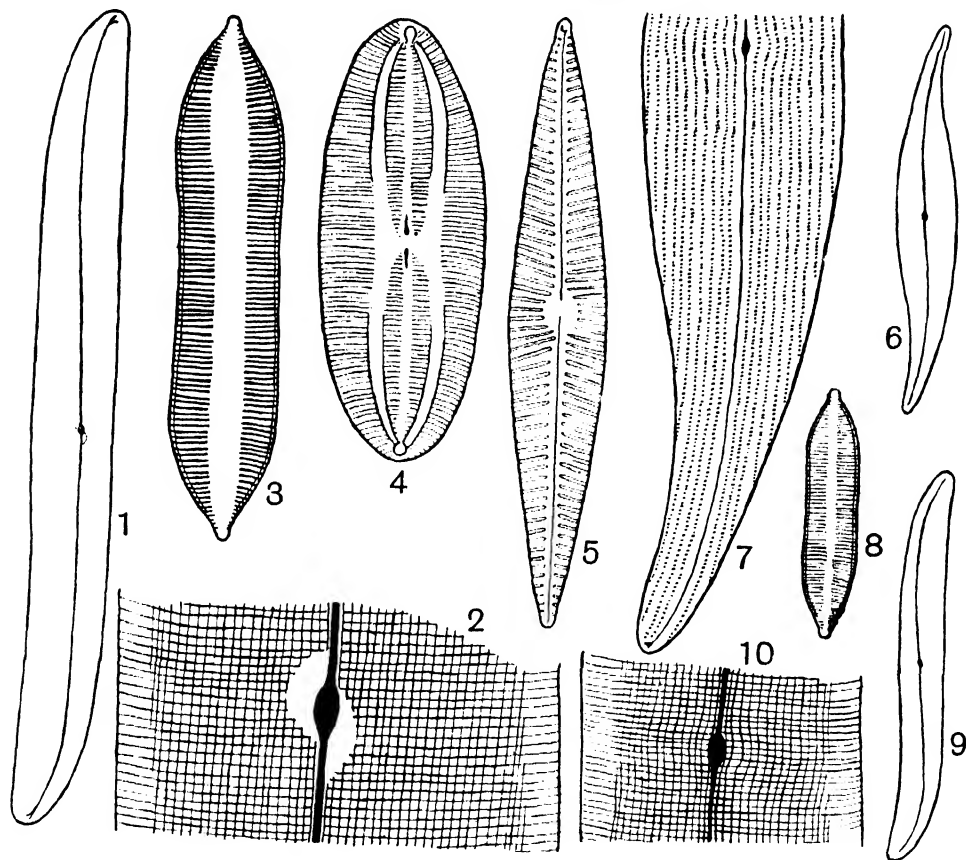
Fig. 21. Diatoms abundant in, and mainly restricted to, the marginal mud, and persisting all the year round. *1, 2, Gyrosigma balticum* Ehr.; *3, Nitzschia acuminata* W. Sm.; *4. Navicula pygmaea* Kütz.[1]; *5, N. spuria* Cl.; *6, 7, Gyrosigma litorale* W. Sm.; *8, Nitzschia apiculata* Greg.[1]; *9, 10, Gyrosigma Wansbeckii* (Donk.)Cleve.*1, 6* and *9*, × 320; *2, 4* and *10*, × 1935; all others, × 963.

56. G. Spenceri W. Sm.

Canvey. A, B, C, D, and E. All the year round.

Ynyslas. C, and F. All the year round.

Fig. 15, *5, 6.*

L. 57–102 μ; B. 8–12 μ; long. striat. 25 in 10 μ; trans. striat. 20 in 10 μ.

This is a very common species and often occurs in great numbers. It is particularly characteristic of the drier zones such as the *Obione* and *Glyceria* zones at Canvey and the Juncetum zone at Ynyslas. At Canvey, however, it was common also at the margins of the marsh, and it often occurred on higher

[1] Not restricted to the margins of the marsh, but more abundant there than elsewhere.

hummocks of accumulating silt in the channels. It is frequent all the year round, but tends to become especially abundant in summer. The most striking record for this diatom was at Ynyslas in November, 1927, when after a very
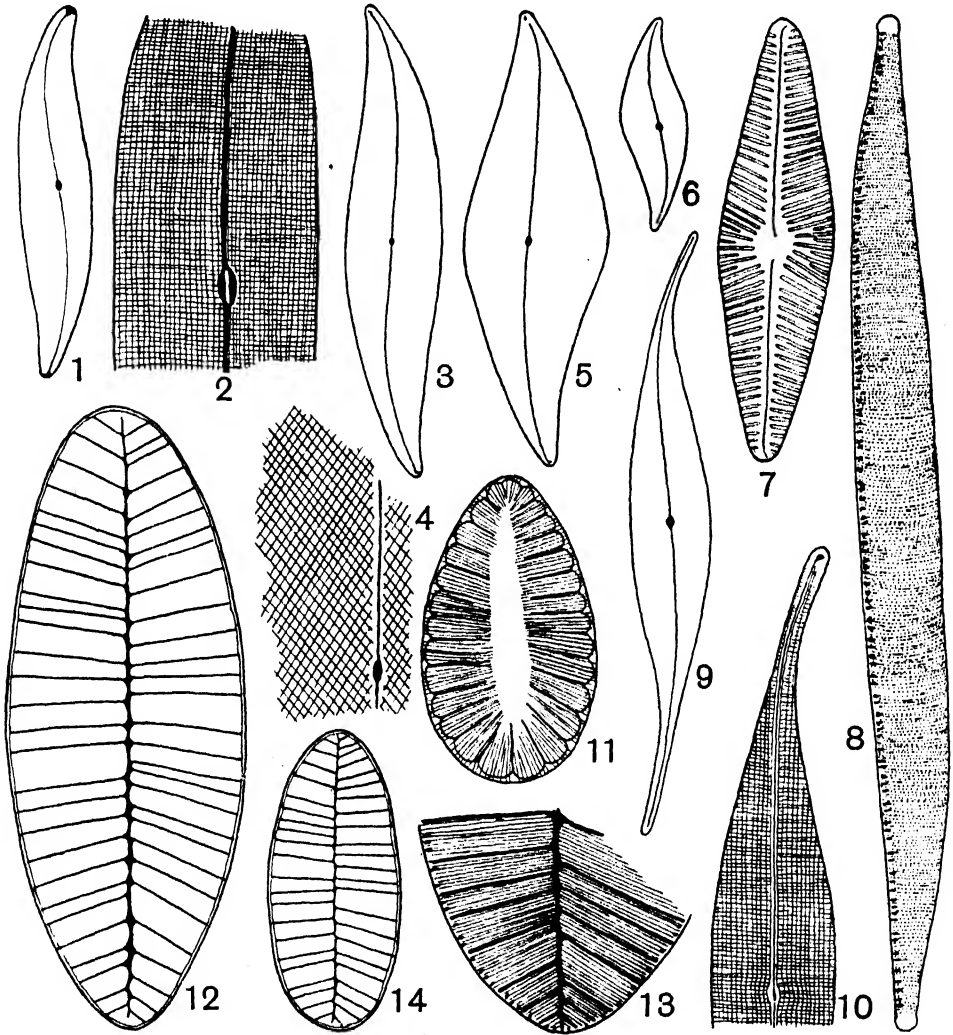
FIG. 22. Diatoms more abundant at the margins of the salt marsh, and in the winter months. *1, 2, Gyrosigma diaphanum* Cl.; *3, 4, Pleurosigma angulatum* Queck.; *5, 6, P. angulatum* var. *quadratum* (W. Sm.) Per.; *7, Navicula digito-radiata* Greg. var. *cyprinus* (Ehr.) W. Sm.; *8, Nitzschia rigida* Kütz.; *9, 10, Gyrosigma Fasciola* Ehr.; *11, Surirella ovalis* Bréb. var. *ovata* Kütz.; *12–14, S. gemma* Ehr. *3, 5* and *6,* × 320; *2* and *4* × 1935; *1, 9, 12* and *14,* × 552; all others, × 963.

high tide, it was very abundant in a brown scum deposited on the turf around each pan at the level at which the water had stood (cf. Carter (**9**), p. 370).

Gyrosigma Spenceri closely resembles *G. Wansbeckii*, from which it is distinguished, however by several features.

57. **G. scalproides** Rabenh. var. **eximia** Thw. (*Pleurosigma eximia* (Thw.)
    V. H.; *Colletonema eximia* Thw.).

Canvey. A, C, D, and E. All the year round.
Ynyslas. F. Fig. 18, *1, 2.*
L. about 68 μ; B. about 10 μ.

This species is especially characteristic of the higher and drier zones, often being an important constituent in the *Obione* and *Glyceria* zones at Canvey, and the Juncetum at Ynyslas. It is rarely found below these levels, except at Canvey, where it is common on the hummocks which rise above the general level of the mud in the channel as a result of accretion. Occurring in tubes, it must be a very important form in helping to stabilise the surface of the soil. No doubt it is fulfilling this rôle when growing on hummocks in the channel, or on soil at the margins of the channel. Although present all the year round it seemed to be more abundant in summer.

58. **G. balticum** Ehr. (*Pleurosigma balticum* W. Sm.).

Canvey. A. Also in plankton of pan. All the year round. Fig. 21, *1, 2.*
L. about 320 μ; B. about 30 μ; trans. striat. 16 in 10 μ; long. striat. 18 in 10 μ.

This is a species very characteristic of the soft marginal mud, being almost entirely restricted to these moist regions. It never occurred in great quantity, merely as isolated specimens. No definite seasonal variation is indicated. The more sandy stretches at Ynyslas are apparently not attractive to it, as it was never found there.

59. **G. Wansbeckii** (Donk.) Cleve (*Pleurosigma balticum* W. Sm. var. *Wansbeckii* Donk.).

Canvey. A, B, and D. No seasonal variation. Fig. 21, *9, 10.*
L. about 150 μ; B. about 18 μ; trans. and long. striat. about 20 in 10 μ.

This is a very frequent species at Canvey, where it often occurs in great quantity. It is very abundant in the marginal regions, preferring the soft wet mud of the unvegetated zones. It was never found above the *Aster-Salicornia* zone, but occurs in the *Aster-Glyceria* zone, which is often very wet and soft. *G. Wansbeckii* is easily confused with *G. Spenceri*, but careful study differentiates between the two. Moreover, there is an ecological difference, *G. Wansbeckii* having a preference for the lower zones, whilst *G. Spenceri* prefers the upper zones, although the last species sometimes becomes quite abundant in the marginal mud.

CYMBELLACEAE.

60. **Amphora Proteus** Greg. in Cleve, II, 1894, p. 103; Peragallo, 1897, p. 200, t. 44, f. 21.

Canvey. A, B, C, and D. All the year round. Fig. 23, *1–4.*
Small form: L. about 23 μ; B. about 7 μ (valve); striae 20 in 10 μ.
Large form: L. about 57 μ; B. about 10 μ (valve); striae 11 or 12 in 10 μ.

Both forms are general in the lower and moister zones, and in the standing water of pans. In the latter habitat they were once found in great abundance in June.

There is some doubt whether these two forms, between which no intermediate individuals were found, really belong to the same species. In fact at first the small form was referred to *A. pusio* Cl. var. *parvula* Floegel (Peragallo (**39**), p. 199, t. 44, f. 10), with which its dimensions exactly agree, the larger form corresponding with *A. Proteus*. If this is the more correct view, there would seem to be few sharp distinctions between the two forms. Apart from its larger size, *A. Proteus* is supposed to be distinct by virtue of the fact that its striations are interrupted in the valve view. A difficulty arises since individuals with the dimensions and striae of *A. Proteus*, but in which there is no interruption, are frequent; again, specimens with the dimensions and striations of *A. pusio* var. *parvula*, but in which there is a distinct interruption in the striae in the valve view, are also frequent (Fig. 23, 3). It would therefore seem that the presence of the interruption is not a good specific character of *A. Proteus*. The question arises whether *A. Proteus* and *A. pusio* var. *parvula* should be retained as forms distinguished by differences of size and strength of striation, the presence of the interruption being regarded as an unimportant variable feature, or whether they should be merged as forms of the same species. Believing that the finer striation of the small form is only the natural result of its smaller size, the writer has chosen the second alternative.

61. **A. lineolata** Ehr. forma.

Canvey. A, B, and D. Also in plankton of pan. VI–IX.
Ynyslas. B, and D. In small channel. III, VII.   Fig. 23, 5–10.
L. 28–46 μ; B. (valve) 6–12 μ.

This form is one which has a conspicuous summer maximum. It is found especially in the lowest zones, and often forms, in warm weather, distinct areas, bright brown in colour and several inches in diameter, on the surface of the mud. Samples taken from such areas at Canvey revealed an almost pure growth of the tiny frustules of this species. The areas are somewhat local, occurring as small groups of circular spots. In the winter such areas would be much more extensive and would consist of *Pleurosigma angulatum* and *Surirella gemma*. The *Aster-Salicornia* and lower zones at Canvey seemed to be a very favourite habitat for this diatom; at Ynyslas it was sometimes found, but not in such great quantity.

The identification of this species presented some difficulties. The view one usually gets is like the girdle view of a *Navicula*, and it is only after very careful study that the slightly bent raphe, which decides that it is a form of *Amphora*, can be distinguished. Often the lateral margins of the girdle view are nearly parallel, a feature which has probably often resulted in confusion with *Navicula complanata* Grun. Furthermore, since the frustules are so very slightly silicified, they become very distorted in the processes of preparation and perfect examples are not easy to find. Sometimes individuals with convex margins in the girdle view are found, and the structure of the valve is best seen from these. A true valve view is almost never seen except in

untreated material. The dorsal side of each valve has very fine striations about 25 in 10μ. The ventral side is also striate in the same way. The girdles are also striate, the dorsal girdle being less finely striate than the ventral. The dorsal girdle had finer longitudinal striations than stated either in Cleve (**10**, II, p. 126) or Peragallo (**39**, p. 225, t. 1, f. 23), who both give 10 in 10μ. The
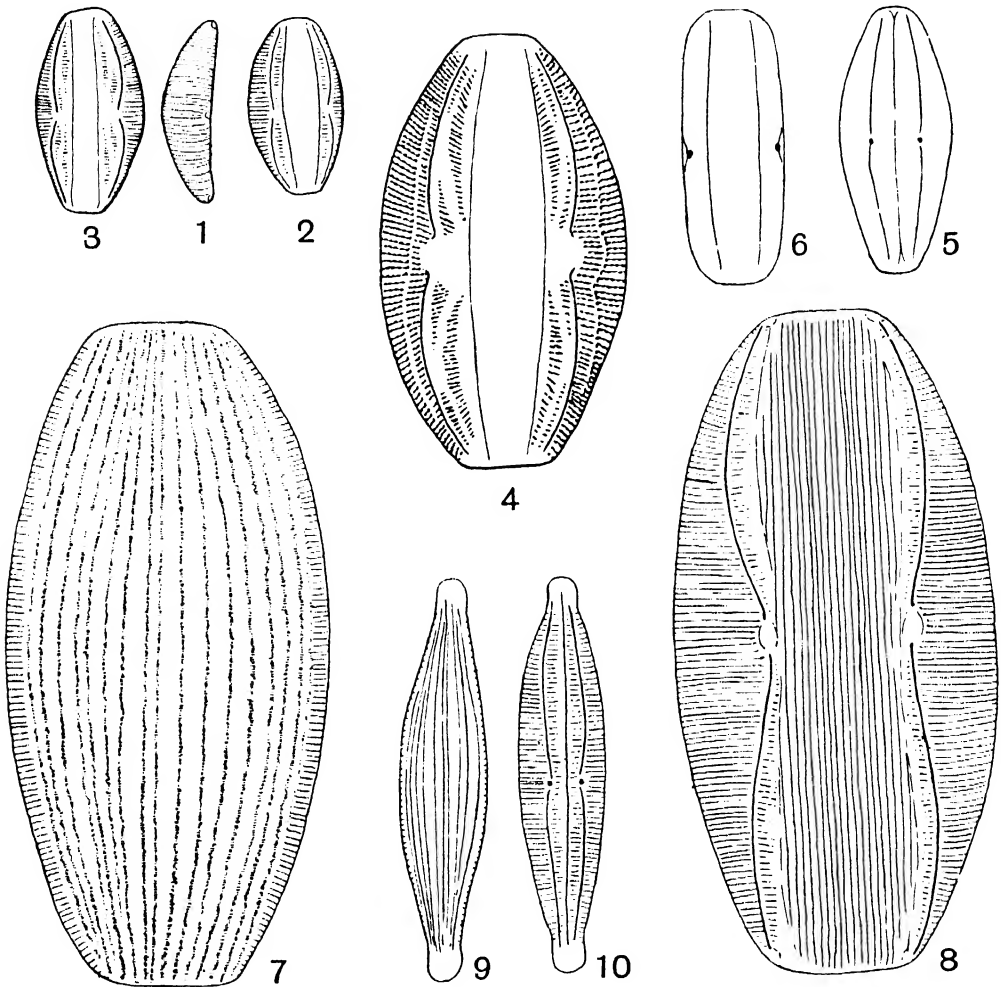
FIG. 23. Diatoms abundant at the margins of the salt marsh and in the summer months. *1–4, Amphora Proteus* Greg.; *5–10, A. lineolata* Ehr. forma. *1–6*, × 951; *7–10*, × 1910.

present individuals showed about 17 in 10μ on the dorsal girdle and the ventral girdle where present showed about 30 longitudinal striations in 10μ. The valve view is almost straight on the one margin, and convex on the other, with somewhat bluntly rounded ends.

This form seems to differ from typical *Amphora lineolata* in the finer striation of its girdles and in its relatively narrower frustules. The above

measurements were taken from perfect frustules. Individuals which have collapsed during preparation frequently have a much greater breadth and much more convex margins in the girdle view than the untreated individual. Such specimens were ignored.

62. **Rhopalodia musculus** Kütz. var. **producta** Grun. in Peragallo, 1897, p. 303, t. 77, f. 23, 24.

Ynyslas. C. vi.
L. about 15μ; B. about 4μ.

This is a tiny species which seems to be quite rare, as it was only observed on one occasion. The apices are not quite so acute or curved as figured by Peragallo.

NITZSCHIACEAE.

63. **Nitzschia navicularis**[1] Bréb.

Canvey. A, B, and C. No seasonal variation indicated.
Ynyslas. D, and F. Also in channels. No seasonal variation indicated.   Fig. 15, 7.
L. about 42μ; B. about 15μ; striae 7 in 10μ.

This is one of the most frequent representatives of the genus though it never approaches *N. rigida* in abundance. It is not sharply limited to the lower zones but was only once found in quantity in the Juncetum zone at Ynyslas, and this was after a very high tide. There is therefore some indication that it prefers the lower levels.

64. **N. punctata** (Sm.) Grun. in Peragallo, 1897, p. 267, t. 69, f. 23.

Canvey. A, B, and D. All the year round.
Ynyslas. In small channel and in pan.
L. about 50μ; B. about 18μ; striat. 9 in 10μ.

This species prefers the moister and lower zones. It never occurs in great quantity, but is an occasional constituent of most marginal samples.

var. **coarctata** Grun. in Peragallo, 1897, p. 268, t. 69, f. 26, 27.

Ynyslas. Large moist channel. Common. vii.

65. **N. apiculata** Greg.

Canvey. A, B, C, and E. Also in plankton of pan. All the year round, but more abundant in summer.
Ynyslas. D, and F. Also in channel.   Fig. 21, 8.
L. 23–30μ; B. about 6μ; striat. 20 in 10μ.

This species seems to have a wide distribution on the salt marsh, not being restricted to any zone. It never occurs in great abundance, however, except in the moister habitats, such as the margins of the marsh, in channels and in pans, and it increases in quantity in summer. The "sillon" in the middle of the valve seems to vary in its breadth, although it is never as wide as in the larger species *N. acuminata*, with which *N. apiculata* often occurs.

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[1] In listing species of *Nitzschia*, the order given by **Peragallo (39)** has been adopted.

66. **N. acuminata** W. Sm.

Canvey. A, B, and D. Also in plankton of pan. All seasons.
Ynyslas. In channel and in pan.
L. about 80μ; B. about 16μ; striae 13 in 10μ.

Fig. 21, 3.

This is a marginal form which seems to require soft mud, and is rarely found higher than the *Aster-Salicornia* zone. At Ynyslas conditions for its development are only found in the small muddy channels and in the mud at the bottom of pans. It is not often present in great quantity.

67. **N. bilobata** W. Sm. var. **minor** Grun.

Canvey. A, C, and E. All seasons.
Ynyslas. D, and F.
L. about 90–95μ; B. about 35μ; carinal dots 6–8 in 10μ.

Fig. 16, *11, 12*.

This species seems to prefer the higher and firmer zones. At Canvey it was only once found in the marginal mud. It is quite frequent as an occasional constituent of the higher zones, though rarely found in abundance.

68. **N. paradoxa** Grun. in Peragallo, 1897, p. 280, t. 72, f. 16.

Ynyslas. Bottom of large channel. Common. VII.

It is rather surprising that this species, known to be so frequent on salt marshes, was only encountered once. The sample in which the specimens were found was collected after a long drought and yielded another form, *N. punctata* var. *coarctata*, which had not previously been collected on the marsh.

69. **N. lanceolata** W. Sm. var. **incrustans** Grun.

Canvey. D, and E. No seasonal variation indicated.
Ynyslas. D.
L. about 50μ; B. about 13μ; carinal dots 5–6 in 10μ.

Fig. 16, *10*.

This is obviously one of the species characteristic of the firmer soil of the higher levels. It seems to be sporadic in its occurrence, but when present it is usually quite an abundant form.

70. **N. subtilis** Kütz.

Canvey. D, and E. No seasonal variation indicated.
L. 25–45μ; B. (valve) 3·5–4μ; (girdle) about 5μ; carinal dots 8–10 in 10μ.

Fig. 16, *1–3*.

The examples of this species were rather shorter than usually recorded (60–100μ according to Peragallo (**39**), p. 286, t. 73, f. 15), but in all other respects they agreed very well. The species evidently prefers the higher zones of the marsh, where it was observed in great quantity, especially in summer. Its occurrence is somewhat sporadic.

71. **N. palea** (Kütz.) W. Sm. var. **tenuirostris** V. H., 1880, p. 183, t. 69, f. 31.

Canvey. E. No seasonal variation indicated.
Ynyslas. F. No seasonal variation indicated.
L. about 50μ; B. about 5μ; carinal dots 12–14 in 10μ.

Fig. 16, *4*.

This is not a common form, having only been observed on three occasions in the present work, and never in great quantity. It seems to prefer the uppermost regions of the marsh. Kolbe (**32**) describes it as being "indifferent" (see p. 172), and Schönfeldt (**42**, p. 159) states that it inhabits the mouths of rivers.

72. **N. obtusa** W. Sm. var. **scalpelliformis** Grun.

Canvey. B, C, and E. No seasonal variation.   Fig. 19, *5.*
L. about $45\,\mu$; B. about $5\,\mu$; carinal dots 8 in $10\,\mu$; striae 25 in $10\,\mu$.

This is a species which flourishes on the stretches of bare firm mud between the phanerogams of the higher zones at Canvey. It seems to multiply abundantly in such localities and often becomes the dominant diatom. Its occurrence is somewhat sporadic and no seasonal periodicity was indicated. It is not found on the softer mud of the channels.

var. ? **nana** Grun. in V. H., 1880, p. 180, t. 67, f. 3.

Canvey. B. VIII, IX.   Fig. 20, *3.*
Valves about $30 \times 4\,\mu$, very slightly sigmoid, carina slightly inflexed in the middle, dots 14–17 in $10\,\mu$, slightly irregular in arrangement, but not appreciably closer or more distant in the middle, striae very fine and close.

This form was only observed on two occasions on the firm mud of the *Aster-Salicornia* zone. On both occasions, however, it was quite abundant, together with other species of *Nitzschia*, including *N. Claussii, N. intercedens* and *N. obtusa* var. *scalpelliformis*. It seemed by reason of its slightly sigmoid valves and carina bent in the middle to fall into *N. obtusa*, but it differs from the var. *nana* of Grun., which is known from brackish waters, in its closer carinal dots (14–17 in $10\,\mu$ instead of 10 or 11 in $10\,\mu$).

73. **N. intercedens** Grun.

Canvey. B, C, and E. VI, IX.
L. about $54\,\mu$; B. about $4\cdot5\,\mu$; carinal dots 7 or 8 in $10\,\mu$.   Fig. 19, *8.*

This species, like the preceding ones, prefers the firmer mud of the upper zones, and it was often very abundant in the almost invisible diatom film which covers areas free from phanerogams and the larger algae.

74. **N. rigida** Kütz. (*N. sigma* W. Sm. var. *rigida* (Kütz.) Grun.).

Canvey. A, B, C, D, and E. Also in the plankton of a pan. All the year round.
Ynyslas. B, and F. Bottom of moist channel and pans. All the year round.
           Fig. 22, *8.*

This species, unlike most of the other species of *Nitzschia* observed, certainly prefers the softer mud of the channels and margins of the marsh. In the upper zones of the marsh it is not infrequently encountered, but it always seems scarce in these localities, whereas in the marginal mud it often becomes exceedingly abundant, and may be the dominating diatom. At Ynyslas it finds its most suitable habitat in the softer mud of the pans and smaller channels, and may occur in quantity locally amongst the phanerogams of the Glycerietum. It is one of the most general diatoms occurring on the marsh, and is likely to be found all the year round. It has been found in quantity both in November and July, but on the whole, seems to be more abundant in winter than in summer.

var. **rigidula** Grun. in Peragallo, 1897, p. 291, t. 74, f. 10, 11 (*N. sigma* W. Sm.
     var. *rigidula* Grun. in V. H., 1880, p. 179, t. 66, f. 8).

Canvey. E (only record). I.

75. **N. Claussii** Hantzsch.

Canvey. B. Also on lump of *Obione* soil fallen in channel. No seasonal variation indicated. L. about 56μ; B. about 5μ; carinal dots 12 in 10μ. Fig. 20, *4*.

When first observed this species was associated with *Navicula scopulorum* living on a large piece of the *Obione* soil which had been loosened by erosion
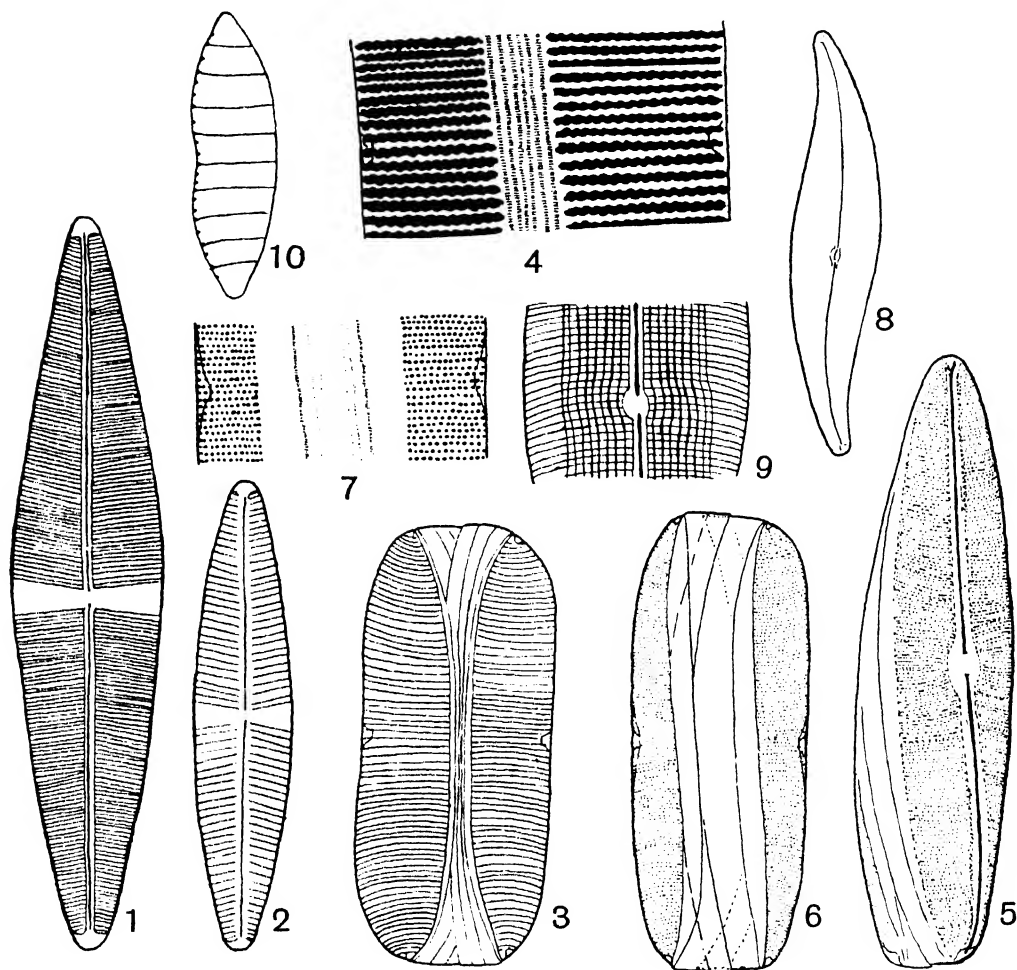
FIG. 24. Diatoms abundant at the margins of the salt marsh and in the summer months. *1, 2, Stauroneis Gregorii* Ralfs; *3, 4, Scoliopleura latestriata* (Bréb.) Grun.; *5–7, S. tumida* (Bréb.) Rabenh.; *8, 9, Gyrosigma attenuatum* Kütz. var. *scalprum* Gail. and Turp.; *10, Nitzschia epithemioides* Grun. 2 and *9*, × 1910; *3, 5, 6* and *8*, × 545; all others, × 951.

and had fallen into the channel several feet below. Although subjected to tidal submergence for several months, the sod remained recognisable for a time, the diatoms also persisting, but later it was washed away. Subsequently this diatom was found in much greater quantity amongst other species of the genus on bare mud in the *Aster-Salicornia* zone.

76. N. epithemioides Grun.

Canvey. A, B, and D. Also in dry mud at the margin of a pan. VI, VIII. Fig. 24, *10*.
L. about 35μ; B. about 10μ; carinal dots 9 in 10μ.

This is a delicate species, only very slightly silicified, and because of this it may perhaps have been frequently overlooked. It is a peculiar fact that its records coincide with those of *Amphora lineolata* on the marsh, also a very slightly silicified species. It prefers the softer marginal mud, and seems to be a summer species. There have been few previous records of its occurrence, and only some of these refer to marine or brackish localities. Peragallo's specimens (**39**, p. 297) were taken from fresh water. In the present case it was never an abundant species, only occurring as an isolated specimen.

77. Nitzschiella longissima (Bréb.) Ralfs var. closterium Ehr. forma,
cf. V. H., 1880, p. 185, t. 5, f. 7, 8; Peragallo, 1897, p. 293, t. 74, f. 15.

Canvey. Plankton of pan. VIII.
Ynyslas. Plankton of pan. VII.
L. about 90μ; B. about 4μ; carinal dots 18 in 10μ.

The accounts of this species are somewhat confused. Van Heurck gives in his description "longueur moyenne $260-320\mu$," whilst the specimens figured by him range from $30-112\mu$ in length. Peragallo gives length $26-140\mu$. The species was not observed on the general salt marsh, only developing in recognisable quantity in the warm water standing in pans in summer. Kolbe (**32**) describes it as "mesohalobic."

<div align="center">SURIRELLACEAE.</div>

78. Cymatopleura elliptica Bréb.

Canvey. A. Very rare. Only record. I.
L. about 90μ; B. about 43μ.

79. Surirella Comis A. S. in Peragallo, 1897, p. 249, t. 59, f. 7.

Canvey. D. Common. Only record. VIII.
L. about 53μ; B. about 43μ.

80. S. gemma Ehr.

Canvey. A, and B. All the year round.
Ynyslas. In small channel. Fig. 22, *12–14*.
Large form: L. about 150μ; B. about 54μ.
Small form: L. about 66μ; B. about 30μ.

This species, like *Pleurosigma angulatum* var. *quadratum* seems to occur in two forms, differing in size, which are not connected by intermediate forms. Both forms are restricted to the lowest regions of the marsh, inhabiting almost exclusively the softer mud at the margins of the channels and becoming very abundant in some of the smaller ones. They also frequently form a dark brown gelatinous film where drainage water from the higher levels of the marsh trickles out, often by way of subterranean channels, into the main channels. It is a decided winter form, reaching its greatest abundance January–March, when it forms a conspicuous brown stratum on the surface of the mud in all

channels. It is sometimes to be found, though usually in very small quantity, in the summer months of the year. The conditions necessary for its development seem rarely to be realised at Ynyslas.

81. **S. ovalis** Bréb. var. **ovata** Kütz.

Canvey. A, D, and E. IX–III.
Ynyslas. B. In large channel and bottom of full pan. In débris around pan. IX–III.
Fig. 22, *11*.

This species seems to be more common in the lowest zones of the marsh, although even there it is not abundant. It is very rare above the *Ast. r-Salicornia* zone. Its restriction to the lowest zones is also revealed in the records from Ynyslas. It seems to be a winter species; there was only one record for it in July, on which occasion it was very rare. This is a common freshwater species, and it is stated by Kolbe (**32**) that it is "indifferent" (see p. 172).

CHRYSOPHYCEAE.

Conrad (**12**) has described a number of organisms belonging to this group from brackish waters in Belgium. Only one representative, however, has been observed during this investigation. The conditions on the marshes, at any rate in the parts under consideration, are undoubtedly too disturbed for the development of these organisms, since nearly every zone is inundated at fortnightly intervals and sometimes more frequently still. The solitary representative was found as a plankton organism in pans of standing water in summer, evidently stimulated to develop in some abundance by the warmth of the water, and the temporary lack of tidal disturbance. Possibly in less disturbed brackish habitats, our flora would be as rich as Belgium in these organisms.

82. **Hymenomonas coccolithophora** Mass. and Conrad in Conrad, 1926, p. 198, f. 15 (*Pontosphaera coccolithophora* Schiller, 1931, p. 192).

Canvey. Plankton of pan in *Glyceria* zone. VIII.
Ynyslas. Plankton of pan in *Glyceria* zone. VI, VII.

EUGLENINEAE.

83. **Euglena limosa** Gard. 1919.

Canvey. A. All seasons.
Ynyslas. A. All seasons.
Fig. 25, *1–3*.

This species was observed in quantity on the soft mud especially at Canvey: it seemed to be most abundant in November–January. Recently an exhaustive analysis of the factors controlling the appearance of this organism on the banks of the River Avon at Bristol has been published by Bracher (**7**). Information from that source indicates that the numbers of *Euglena* tend to go up in May, and that during the greater part of the summer the organisms are present to the amount of 75–85 per cent. of their maximum development. It was impossible to compare the occurrence of *Euglena* at Canvey with this periodicity described by Dr Bracher, since in the present case *Euglena* does not occur in

such abundance as on the Avon. Undoubtedly Dr Bracher had ideal conditions for studying the periodicity of *Euglena* on the Avon banks, where it forms conspicuous stretches of almost continuous green for long distances along the river bed, whereas at Canvey, at its highest development, it is only represented
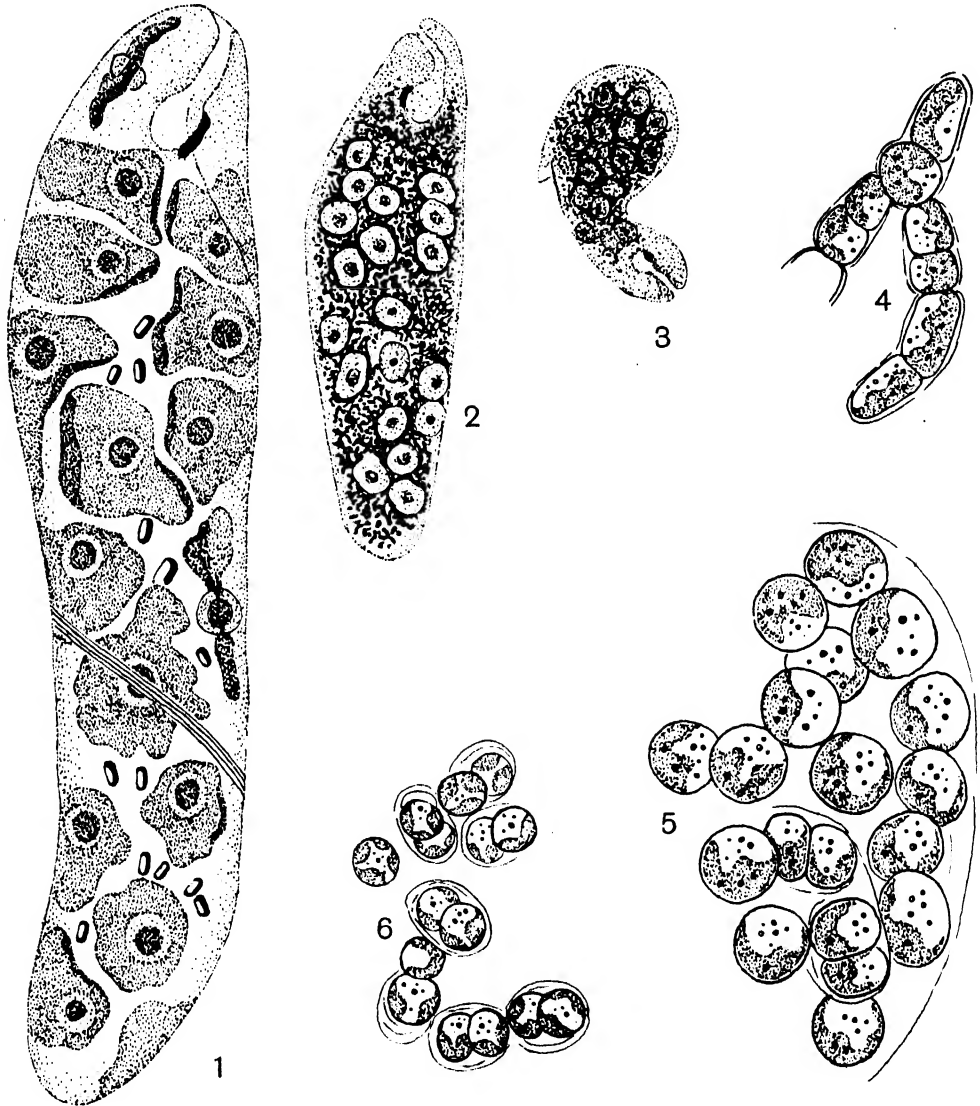
FIG. 25. *1–3, Euglena limosa* Gard. In *1* the striation of the periplast is only indicated in one spot; *4–6, Phaeococcus adnatus* (Näg.) West. *1*, × 1070; all others, × 613.

by small isolated green patches which might easily be overlooked in the field and give the impression of sporadic appearance. *Euglena* was observed on a few occasions at Ynyslas, but it was very much rarer than at Canvey and was not often visible in the field. Certainly neither at Canvey nor at Ynyslas does *Euglena* play such an important part as it does on the banks of the Avon.

Having had the opportunity, owing to the courtesy of Dr Bracher, to examine the Avon material, the writer is entirely in agreement with her that the form which occurs in the Avon bed and also at Canvey and Ynyslas, is identical with *E. limosa* described by Gard (**19, 20**). The same form has also been observed by the writer from other brackish localities around our coasts. Unfortunately Gard's description is not accurate, particularly with reference to the chloroplast, which is not a network, as he believed, but is really composed of a number of plates, separate from each other and with their margins frequently turned over (Fig. 25, *1*). Each plastid contains a pyrenoid with two distinct lens-like portions to its sheath, and the protoplast is full of rod-shaped paramylum granules. Owing to the dense nature of the protoplast, it is not easy to make observations on the organism, but by the careful examination of favourable individuals, having little paramylum and less pigmentation, such as one encounters occasionally in looking through abundant living material, the true nature of the plastids can be made out with ease. The study of such occasional favourable living individuals is far more convincing than preparations of fixed and stained material. Thus it seems proved that so far as its plastids are concerned, *E. limosa* resembles *E. deses*, a species with which it has previously been confused (Bracher (**6**)). Gard believed that the plastid of *E. limosa* was one of the most important features distinguishing it from *E. deses*. Although resembling the latter species in its plastids, however, *E. limosa* is still distinct from it in several other features, namely (1) absence of flagellum, (2) nature of the sheath of the pyrenoid, and (3) absence of short point at the distal end.

CRYPTOPHYCEAE.

84. **Phaeococcus adnatus** (Näg.) West in Cotton, 1912, p. 82 (*Gloeocystis adnata* Näg.).

Canvey. Escarpment between C and E. All seasons.
Ynyslas. Marginal and inland escarpments, and around the margins of pans; amongst the turf in C, D, E, and F. Fig. 25, *4-6*.

This alga is imperfectly known, as it has not been figured in recent times. Its true systematic position will be uncertain until its life history is fully worked out. Pascher (**37**, p. 528) has instituted a new genus of Chrysophyceae, *Apistonema*, to include another alga previously ascribed to *Phaeococcus* (*P. Clementi* Borzi), and a second species, *Apistonema pyrenigerum* has recently been described (Pascher (**38**)). In its tendency to form short filaments, *Phaeococcus adnatus* is very reminiscent of the last, and it is possible that future work will prove it to be another member of the genus *Apistonema* (cf. Fig. 25, *4*).

The alga was more common at Ynyslas, where it seemed to choose localities not too frequently inundated by the tides. It rarely occurred in great quantity. but was a frequent constituent of algal masses in the upper zones. Cotton (**14**) found that this alga formed a very characteristic stratum on vertical peat

banks at Clare Island. On the Welsh marsh it was never macroscopically visible, occurring usually as a subsidiary form amongst other algae. At Canvey it was only found on a few occasions.

PHAEOPHYCEAE.

A considerable amount of work has already been done on the salt marsh Phaeophyceae (see Baker (**2, 3**)). It is a rather peculiar fact that very few of the forms described by Baker occur either at Canvey or Ynyslas. The great masses of fucoid growth described by that author in the *Salicornia* marshes at Blakeney, and the allied forms reported to be associated with *Glyceria* and *Armeria* turf at Clare Island (Cotton (**14**)) are entirely wanting in the two marshes described here. Apart from somewhat transitory growths of Phaeophyceae in the marginal zones of both marshes in spring, the Juncetum at Ynyslas is the richest habitat. At Canvey, salt-marsh fucoids have not been observed at all, and at Ynyslas, although they occur on brick walls and on soil near the outlets of various streams running into the estuary, they do not form part of the true salt marsh vegetation except in a limited part of the Juncetum zone. It is stated, however, by Baker (**3**, p. 373) that fucoids disappear in well established saltings. This may account for their absence in the present instance.

ECTOCARPACEAE.

Forms representing this family were not infrequent on both marshes, but the greatest difficulty was experienced in identifying them. It seems probable that two species are represented, *Pylaiella litoralis* (L.) Kjellm. and an unnamed species of *Ectocarpus*. I am greatly indebted to Dr Margery Knight for very generously devoting considerable time to samples of these algae. She reported that in most cases accurate identification was impossible, since in practically every instance only the basal creeping part of the plant was represented, and the specimens, far from growing luxuriantly, were only just existing in the salt-marsh habitat.

In morphology, the algal filaments were about 20–30μ in diameter, the cells were usually about as long as broad, or sometimes shorter or up to twice as long. The form on the Canvey marsh was usually unbranched or only sparsely branched, as were also the plants from the higher zones at Ynyslas. The marginal escarpment of the latter marsh, however, produced specimens richly branching and with attenuated branches. There was usually a rhizoidal basal attachment poor in plastids and often richly branched. The vegetative part of the plant consisted of cells possessing a number of small discoidal plastids, which were sometimes drawn out into ribbon-like bands. A nucleus was often visible in a transverse bridge of protoplasm stretching across the cell.

On both marshes the algae were most prominent in early spring, though fragmentary samples have been collected in October and they may be represented in some quantity even as late as July. In late winter and in spring,

however, the margins of the marsh were frequently festooned with abundant brown filaments, clinging together in masses of considerable thickness. At Canvey, it was chiefly the *Aster-Salicornia* zone which was affected, the small escarpment between this and the stretch of marginal mud being clothed with the brownish covering. In January, 1928, the *Aster-Salicornia* zone itself showed areas of considerable size of a brown alga, almost pure. In the following March, this became overgrown with *Enteromorpha* (see Carter (9), p. 357). Very rare fruit showed that the alga in question was an *Ectocarpus*, but
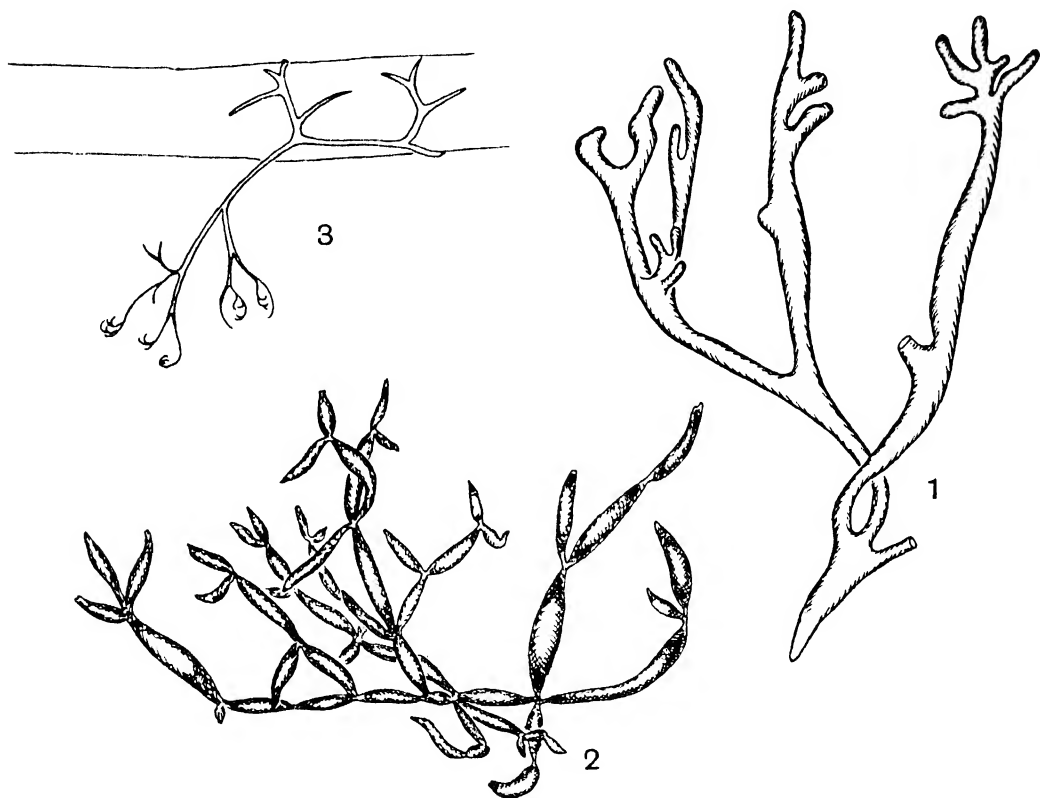
FIG. 26. *1*, ? *Pelvetia canaliculata* Deene et Thur. ecad *muscoides* Skrine, × 8; *2*, *Catenella opuntia* Good and Wood, × 6; *3*, *Bostrychia scorpioides* Mont., a small plant attached to stem of *Obione*, × 5.

Dr Knight said it was not possible to name the species. Filaments of a brown alga were also rare in the *Obione* and *Aster-Glyceria* zone, but not in the *Glyceria* zone.

At Ynyslas the marginal escarpments seemed to be the chief habitat of brown algal festoons. This produced rare fruit in May, 1928, and Dr Knight was able to identify it as *Pylaiella litoralis*. This form was abundantly branched, with piliferous branches. Fragments of the unbranched form such as was found at Canvey were occasionally observed in the Glycerietum and Juncetum of the Ynyslas marsh, and in August, 1928, specimens from the Juncetum

showed rare plurilocular sporangia which again proved the alga to belong to the genus *Ectocarpus*.

The evidence indicates, therefore, that at Ynyslas at least two algae belonging to the Ectocarpaceae are represented, *Pylaiella litoralis* and an *Ectocarpus*, whilst at Canvey only an *Ectocarpus* has been distinguished. At the same time it is quite possible that *Pylaiella* also occurs at Canvey, since in the absence of fruiting specimens it is impossible to distinguish the two forms.

SPHACELARIACEAE.

A brown alga was found to be fairly general in the Juncetum zone at Ynyslas, and also occasional on the upper margins of channels, sometimes being very pure and abundant locally, especially in summer. Its filaments were abundantly branched, about 25–40μ in diameter, and the cells are initially about as long as broad, but subsequently show frequent longitudinal septation, except at the tips, where the large apical cell characteristic of this family could be distinguished. It formed a compact growth of upright tufts closely packed together. Dr Knight very kindly confirmed its being a member of this family, and suggested that it might be *Sphacelaria radicans* Harv.

FUCACEAE.

The only representative of this family is a small alga which has a rather local distribution on the Ynyslas marsh. It appears to be a form of *Pelvetia canaliculata* Decne et Thur. Dr J. S. Bayliss Elliott, who was studying the fungus flora of the marsh during the early part of this investigation, was the first to notice its occurrence and the fact was published in the following year by Skrine (**43**), the alga being identified with *Fucus vesiculosus* L. ecad *muscoides* Cotton. Subsequently the alga was placed under the *Pelvetia canaliculata* as ecad *muscoides* of that species (Skrine (**44**)).

The alga is to be found in the most typical part of the Juncetum zone. To the south of the area, where there is a certain amount of coarse grass amongst the *Juncus* plants, which are rather separated from each other, it does not occur. Although local, it seems to flourish and may even invade the grassy sward of the adjacent Glycerietum or Armerietum. The plants are erect, and, having no mechanism for attachment at the base, are merely imbedded in the soil (Fig. 26, *1*). No reproductive bodies or endophytic fungus were observed[1] (cf. Sutherland (**47**); see also Part III).

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[1] It is possible that a more prolonged search might have revealed the presence of the fungus, but the writer has not thought its absence sufficient evidence for removing the alga from *Pelvetia canaliculata*, since the examination of another undoubted form of this species, collected in the neighbouring outlet of the River Leri at Ynyslas, also failed to reveal the presence of the fungus. At the same time the writer has suspicions that the alga from Ynyslas may be identical with that described by Cotton. It has been compared, both morphologically and anatomically, with Cotton's original specimens from Clare Island, and no differences could be distinguished. The presence of the endophytic fungus does not seem to be a reliable test for distinguishing *Pelvetia* from other Fucaceae, and there does not seem to be any other way of identifying these marsh forms of *Fucus* or *Pelvetia*.

RHODOPHYCEAE.

The Rhodophyceae are represented on the two marshes by two species, *Catenella opuntia* Good and Wood (Fig. 26, 2) and *Bostrychia scorpioides* Mont. (Fig. 26, 3), both already well-known salt-marsh algae. At Ynyslas, both forms are confined to the Juncetum zone, where they form short erect tufts about 1 cm. high, clustered around the base of the *Juncus* plants. At Canvey, *Catenella* is absent, but *Bostrychia* is considerably better developed than at Ynyslas, since it forms loose tangles several inches in diameter, resembling coarse black hair, loosely anchored on the *Obione* plants of the *Obione* zone or entangled around the grass haulms of the *Glyceria* zone. The lower zones of the marsh are quite free from *Bostrychia*.

An unnamed species of *Porphyra* is found at times on the lower parts of the marsh, especially in the *Aster-Salicornia* zone, its membranous fronds stranded over other algae in such a way as to make it difficult to decide whether the plants are really growing there or whether they are left behind by a receding tide. On the whole the latter seems more likely.

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(To be concluded.)

A SUGGESTED EXPLANATION OF THE PREVALENCE OF VIVIPARY ON THE SEA-SHORE

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ONE of the most well-known and noteworthy features of the mangrove forests is the habit of germination of the seeds on the parent trees themselves, but the exact cause of this prevalence of the viviparous habit on the sea-shore is not so well understood. In fact, recent work seems to shake our faith in all the old hypotheses, even though no recent worker has suggested any new one that would explain away the various objections against the older. Some of the recent workers have, however, expressed their inability to understand some points on the basis of the old theories (**8**).

The old explanations of the prevalence of vivipary on the sea-shore can be easily grouped into two classes. According to Guppy (**2**), vivipary is a relic from the past, when this habit was the rule under the uniform climatic conditions then prevailing over the globe, while "ovipary" or what we regard as the normal germination of the seeds after detachment from the parent plants, is an adaptation to modern conditions which set in with the differentiation of climate. He thinks that the mangrove swamp still retains the climatic conditions once general over the globe, and for this reason one still finds the viviparous habit retained by a fairly large number of plants of that habitat.

Guppy's hypothesis, however, is open to strong objections and it has never been accepted by any large majority of botanists. Palaeobotany has nothing to say in its support. The belief in the uniformity of climate in early geological times, also, now seems to have lost foundation, and as Seward (**6**) says in his recent book, "It is inconceivable that the world can ever have had a climate that was uniform."

On the other hand, Schimper, Warming and Haberlandt regard vivipary as an adaptation to environment, providing the species with a means for dispersal, anchoring and establishment of the young plants (**3, 4, 5, 7**). This belief is based chiefly on the fact that the Rhizophoras, in which the phenomenon of vivipary is most remarkably displayed, were regarded by these authors as the pioneers of mangrove formations. The wide distribution of these, and of other mangrove species which show vivipary in less marked degree, and the supposed ability of the former to act as pioneers in starting new forests, was directly attributed to the viviparous habit. Later work, however, extending over several years by forest officers in Malaya, the Philippines and elsewhere, has shown that the thesis based on earlier observations was not well founded (**1, 8**).

It had been based on short excursions to Singapore and its neighbourhood, a region which, according to Watson, "has suffered from chronic over-exploitation and constant interference with drainage."

In the mangrove forests of Malaya, it has now been shown that species of *Avicennia* and *Sonneratia*, and not the Rhizophoras, are the pioneers in the formation of new mangrove forests. Of these, the *Avicennia* is only semi-viviparous, while the seeds of *Sonneratia* are neither viviparous nor armed with any other anchoring device. Yet *Sonneratia*, says Watson, is the first to appear on many banks that "are often entirely isolated and may be some miles out to sea, the young trees being at first completely submerged twice daily, except during neap tides." Watson has also shown that it is necessary for the banks to remain uncovered for several days before any form of land vegetation can develop and this affords ample time for even the non-viviparous seeds to germinate and fix themselves in the soil. These conclusions are entirely supported by Brown and Fischer's work in the Philippines and also by that of Becking, Berger and Minderma[1]. These authors have shown that the silt deposits remain bare until they have attained very definite conditions of elevation and consistency, and that mangroves follow silting rather than cause it.

Thus the viviparous habit seems to be of no particular importance to a species in enabling it to act as a pioneer by aiding dispersal and anchoring of the young plant; and its absence does not present any serious obstacle to the dispersal and establishment of a species under the peculiar conditions of the sea-shore. The only possible use of the habit in this connection would be an earlier start of the growth of roots in the soil: thus viviparous seeds would be theoretically better able to establish themselves on a tidal coast. In actual observation, however, there is no evidence of this. We find non-viviparous Sonneratias not only successfully competing with the viviparous Rhizophoras and Bruguieras, but actually superior to them in power of establishment on new silts. The latter can grow only on silt that has been enriched by the less exacting Sonneratias and Avicennias, even though they ultimately displace the pioneer species.

Has vivipary, then, any particular use, and why should it be so common on the sea-shore? In my opinion, an answer to this question is to be sought in quite different quarters. Recent ecological work has shown that while many plants can grow in a saline soil, their seeds cannot germinate in such a soil—the salt solution hindering the water absorption which is always essential for the germination of the seeds **(9)**. And Guppy **(2)**, experimenting with the buoyant seeds of tropical and British littoral plants belonging to the families Leguminosae and Convolvulaceae, found that the seeds of such species when placed in the sea and fresh water respectively, absorbed water in both cases, swelled and sank, those in fresh water proceeding at once to germinate at the bottom, while those that sank in sea water merely decayed, showing

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[1] Quoted by **Watson (8)**.

conclusively, that the seeds can germinate only in the absence of strong concentrations of salt.

The seeds of most inland halophytes germinate, most probably, only after good rains when the soil solution is very much diluted, but such a thing is not possible in the mangrove swamp and on the sea-shore. Rains make no difference there and the salt-content of the soil remains high and approximately uniform throughout the year. Vivipary or the germination of the seeds on the parent trees themselves is the only method by which the injurious action of the salts of the soil on the seeds, preventing them from germination could be avoided and it appears that this is the reason that plants with a viviparous habit have gradually become grouped on the sea-shore. The habit probably arose independently in the different plants in different localities as a variation from the normal due to environmental effects or some other unknown causes, as is fully proved by the occasional occurrence of vivipary in land plants in places remote from the sea. Of these species, the halophytic gradually shifted to the sea-shore where this habit proved really useful and, under the uniformly warm and saturated atmosphere of the tropical littoral lands, the original variations became a regular habit with the species. This habit is still very strong in the various mangrove species because it is really useful to them in tiding over one of the greatest obstacles in their environment.

I do not know if this explanation has been put forward by others, but Blume[1] may have had similar ideas in his mind, when he wrote that "the fruits of *Nipa fruticans* are not separated from the head before germination is so far advanced that sea-water no longer injures the seedling." On the whole, however, this explanation appears to me much more attractive than the old hypothesis of adaptation to dispersal and anchoring of the young plants. Viviparous seedlings may be fulfilling these functions to some extent, but the main reason that this habit is so well represented on the sea-shore is to be found in the fact that it enables these plants to overcome one of the greatest obstacles in their environment. There is no other method of avoiding the injurious action of the salt water of the soil which prevents the seeds from germinating.

An objection, however, can be raised against the present explanation with regard to the Sonneratias and some other plants with non-viviparous seedlings which grow as well on the sea-shore as the viviparous species. One may ask for an explanation of their presence on the sea-shore. In my opinion these plants are to be regarded as extreme halophytes which have become so well adapted to their environment that their seeds have acquired the power of germination in a saline soil.

The explanation given above is to be regarded as only, till it is proved or disproved by experiment, a task which can be accomplished by those alone who have easy access to mangrove forests.

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[1] Quoted by **Guppy** (2).

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NOTE ON THE OCCURRENCE OF *SALIX* IN TEMPERATE SOUTH AMERICA

In a paper published in *The Journal of Ecology* in 1922 (**10**, 62–86) I referred to the occurrence of *Salix humboldtiana* in temperate South America at or near the latitude of Buenos Aires, approximately the latitude of Cape Town, to which point the genus ranges in South America. In an interesting paper on the vegetation of Patagonia ("Étude phytogéographique de la Patagonie," in *Bull. Soc. Roy. Bot. de Belgique*, **58**, 105–80, 1926), Prof. Lucien Hauman refers to the occurrence of *Salix humboldtiana* as a riparian shrub in the "Monte," where the vegetation is entirely xerophilous, consisting essentially of a shrubby growth 1–4 m. high, though in certain areas developing into true trees. He mentions the occurrence of this willow as far south as the lower reaches of the River Chubut. This river is approximately in 44° of south latitude, which is 9° farther south than Cape Agulhas, in South Africa. The actual statement (p. 164) is: "Je ne connais pas personnellement le cours inférieur du rio Chubut, mais je me suis assuré que ses rives sont encore occupées par des petits bois de *Salix Humboldtiana* (Pl. I), ce qui est pour moi caractéristique du Monte." The photograph (Pl. I, fig. 2) shows a dense growth of shrubs fringing the stream. J. Burtt Davy. December 17th, 1932.

LETTER TO THE EDITOR

PHAEOCYSTIS AND HERRING SHOALS

To THE EDITOR of *The Journal of Ecology.*

SIR,

In his paper on this subject (*Journal of Ecology*, Vol. **20**, pages 326-340), which was a lecture delivered at a meeting of the Society at Lowestoft on May 22nd, 1931, Mr Savage expresses his personal opinion that *Rhizosolenia* has not much influence on the shoaling of the herring in English waters. He refers to a forthcoming paper to be written in collaboration with our former colleague, Professor A. C. Hardy, Department of Zoology and Oceanography, University College, Hull, in which the general question of the influence of phytoplankton on the herring will be treated in full detail. Subsequent discussion with Professor Hardy has brought out the fact that he does not agree with Mr Savage in the provisional opinion expressed, but ascribes to *Rhizosolenia* a much more important role. The object of this note is, in fairness to Professor Hardy, to put on record his caveat. In a complicated problem of this kind there is naturally still room for some divergence of opinion, and it is fortunate that such close and friendly relations exist between the two workers as to render possible effective co-operation both in the collection of data and in the publication of results. It is, of course, common knowledge that Professor Hardy, when a member of the Ministry's staff, was the initiator of this important line of research, and since his appointment at Hull he has been actively engaged in following it up on his own lines, in close association with the Ministry.

I am, Sir,

Your obedient servant,

E. S. RUSSELL,

Director of Fishery Investigations.

REVIEWS

THE WATER RELATIONS OF PLANTS

Walter, H. *Die Hydratur der Pflanze, und ihre physiologisch-ökologische Bedeutung.* (Untersuchungen über den osmotischen Wert.) Pp. 174 + xii; 73 figs. Price RM. 10. Gustav Fischer, Jena. 1931.

Elementary text-books of physics sometimes endeavour to explain the idea of temperature to schoolboys by means of the hydrostatic analogy, though when this is done it is usually thought wise to add a caution against the dangers of the comparison if it should be carried too far. Prof. Walter has thought it worth while to try and explain to botanists the complex relations between plants and water by reversing this analogy, and while doing so has forgotten, we are afraid, the recommended foresight and caution. T. H. Huxley has often been considered a model to biological writers, and his sparing use of similes has been remarked upon. "Since accuracy and veracity were the qualities at which he consistently aimed, Huxley," his grandson tells us, "was sparing in the use of images. Ideas can be very vividly expressed in terms of metaphor and simile; but, since analogies are really complete, this vividness is too often achieved at the cost of precision. Seldom, and only with the greatest caution, does Huxley attempt anything like a full-blown simile." The complete lack of reserve with which Prof. Walter's analogy is to be applied may be inferred from the title, and is made entirely clear as early as the sixth page by the following definition italicised by the author. "In Analogie zum Wärmezustand—der Temperatur—schlagen wir für den Wasserzustand die Bezeichnung Hydratur vor." Since heat potential is called temperature, the corresponding factor in relation to water, supposing it to exist, must, apparently, be called hydrature. The author hastens to admit that this very unpleasant word is not, philologically speaking, all that it might be: botanists, however, will probably reserve their principal objections rather for its redundancy and misleading suggestions.

The author desires to describe, quantitatively if possible, the relation between living matter and its contained water. He even goes so far as to hint that this relationship has been overlooked in the past, a suggestion that, whether he agrees or disagrees with ideas such as the "fixed water" concept of Newton, Gortner and others, seems quite indefensible. Having invented "hydrature," however, it is not altogether surprising that the author should tend to regard water relations solely in terms of his analogy, and to suppose that the rules for heat relationships must necessarily apply to relations with water. The danger of this position is soon appreciated. Had the author referred once more to his text-book of physics he would have found the temperature of a body defined as the average kinetic energy of its molecules. When heat passes from one piece of matter to an adjacent piece no molecules need be transferred, merely the energy lost and gained in a number of molecular impacts. When on the other hand water passes from some one body to another a transference of the molecules themselves is occurring, a process of an entirely different physical character. It follows from considerations of probability, that the movement of heat must depend on the temperature difference, i.e. the difference of average kinetic energies of the molecules of the substances concerned. In cases where the transfer of water is molecular it will be similarly related to the difference of vapour pressures above the two absorbing bodies, but in this connection it must not be forgotten that, while temperature is the expression of an average kinetic energy of all kinds, rotational and vibrational as well as translational, the vapour

pressure depends on the number of molecules and their translational velocity alone. It is, nevertheless, such similarity as there is that has led our author into his error. What he would do on his analogy with mass movements of water it is impossible to imagine.

As a measure of "hydrature" relative vapour pressure is proposed, and it is a little strange that the mention of the word pressure did not sound a warning. Any sort of pressure acting on water must affect its relations with absorbing substances, whether it acts molecule by molecule, as in diffusion or osmosis, or whether it is applied mechanically in the mass, as by the walls of a retaining vessel. The generalised conception required to cover the whole of these relations is neither suggested by the word hydrature nor defined by its definition. Even if it were the invention would be unnecessary, for a suitable term has already been in existence, and even in common use among botanists, for some years. In order to correct certain misconceptions Ursprung has recently recapitulated his idea of "Saugkraft" (*anglicé*— suction force or better suction pressure) in the following words ". . .definierte ich die Saug-kraft einer Zelle als die Kraft, mit der die Zelle Wasser einzusaugen strebt." It was also made perfectly clear that the term was considered applicable to soils, solutions, and, indeed, to any other absorbent body. This term rests on no dubious analogies, is in accord with current physical terminology, and is universal, that is to say completely independent of the particular mechanisms of individual cases. The last is a requirement that Prof. Walter himself emphasises.

The stated object of this book is not, however, to review the movements of water into absorbing bodies, but the static relations between absorber and absorbed; and the author appears to think that, whereas "Saugkraft" is concerned with the former, "Hydratur" describes the latter. How this idea could have arisen, and how it survived the attempt to apply it in detail it is difficult to understand. The most general quantitative relationship between water and the varied substances with which it is connected in plants is the force by which it is held to them. Having said so much it is obvious that the correct measure of the quantity is Ursprung's "suction force" expressed in any convenient units. Any further exploration of this field must depend on a consideration of the individual mechanisms at work, hydrostatic, osmotic, imbibitional, capillary, etc., an adventure that the author expressly eschews.

It was pointed out by Ursprung and Blum that the suction pressure of a mixed solution might be measured by the vapour pressure with which it is in equilibrium, and as already mentioned it is relative vapour pressure, that is also chosen as a measure of "hydrature." This pressure is often conveniently determined with the help of the formulae that connect it with osmotic pressure, lowering of the freezing-point, etc., and so by easy stages we come back to the old conception of the "osmotic value" as the dominant factor in the water relations of the cell. The greater part of the book is, in fact, a review of the extensive literature of this subject. A new idea is introduced, however, when it is suggested that the osmotic value of the cell sap indicates, not only the water condition of the sap itself, but also that of the cytoplasm. It is thought, that is to say, that the two regions existing side by side must keep themselves in equilibrium. This idea is fundamental to the whole of the work that follows, yet nothing whatever is done to make it acceptable. No data are presented bearing on the rate of adjustment, and it is hard to believe that Prof. Walter has ever examined a curve representing the approach of a plant tissue, seed, or relatively simple colloid, immersed in a solution towards a water equilibrium. The system may be measurably out of adjustment for many days, whereas the osmotic pressures of saps, especially those of leaf cells during assimilation, may vary erratically within the hour (p. 47 *et seq.*). An analogy is also drawn on p. 6 between the imbibitional and capillary effects of the soil and the similar effects inside a plant. It is, however, known that the establishment of an equilibrium between soil moisture and the vapour pressure at the surface of the soil may be delayed for more than

three weeks (Keen, *Physical Properties of the Soil*), an inconvenient fact the author seems to have neglected.

This exposition of water in relation to plants, so unfortunate in its inception, gains little in its detailed application. An author who states at the outset "Der Boden...zeigt stets eine hohe, ziemlich konstante Hydratur," i.e. relative vapour pressure, "um 100 herum," has only himself to blame if the reader's confidence begins early to wane. To follow the chain of the argument further, and pick out its weaknesses link by link, would be a wasted labour; two points of fairly wide application must suffice.

The concepts of minimum, maximum and optimum "hydrature" are used to define the range of a plant's toleration and response towards water. Only the most meagre information is given, however, about the experimental methods of securing these conditions, and the tables of results usually tell us nothing at all as to the number of determinations on which their figures are based. Considering the nature of the work, and its ecological application to plant populations, it is hard to see what value these results, some of them admittedly unduplicated, can have apart from any estimate of error. The difficulty of fixing the "cardinal points" is much increased, we are informed, by their variability, a shortcoming they share with those for temperature, and we are tempted to suppose that the author only sees in this a further support for his hydrothermal analogy. It has, of course, been realised since 1905 that the cardinal point system of expressing temperature and some other physiological results is of very limited use, and it seems a pity to revive it in a new connection. The ecological end in view, viz. that of classifying plants according to the range of their osmotic values, would probably have been better served by the normal statistical method of determining the means and standard deviations of these quantities.

The rate of drying out may have a very marked effect on the "hydrature" value at which the plant succumbs (p. 101). This seems a direct frontal attack on the value of "hydrature," at least as determined, as an expression of the cytoplasmic water relations. The author seems, however, in no way disconcerted by this awkward fact, merely commenting on the hardening of plants raised in warm houses by graded changes of temperature.

It has happened before that a book written to prove a case has survived as a repository of data. Any utility this book may have must be of this kind, for which reason we are left wishing all the more strongly that there had been some estimate of the reliability of the data. In the absence of this, and in the face of the unsoundness of its theoretical basis any attempt to apply "hydrature" to the solution of ecological problems seems stultified at the outset.

W. O. J.

PEDOLOGY

Robinson, G. W. *Soils: their Origin, Constitution and Classification: an introduction to Pedology.* Pp. xv + 390, with frontispiece and 12 figs. in the text. Price 20s. net. Thomas Murby and Co., 1 Fleet Lane, London, E.C. 4. 1932.

This is a welcome introduction to the modern science of pedology, which is practically a child of the present century and is now developing with great rapidity. The book can be highly recommended to plant ecologists, whose work depends so largely on an appreciation and knowledge of soils, as an authoritative and systematic treatment of the subject.

The introductory chapter emphasises the modern standpoint, which takes the whole soil "profile" as seen in the field as the proper unit of study, and regards the laboratory analysis of samples as a means of elucidating the nature of the profile. Subsequent chapters deal with

the Constitution of the Soil, the Pedogenic Processes, the Clay Complex, Exchangeable Bases, Organic Matter, General Physical Properties, and Water Relationships. Particular types of soil are considered in the next chapters, and then Classification, the Geography of Soils, Surveys, Analysis, Relation to Plant Growth and Agriculture. An appendix gives an account of methods of analysis. The modern standpoint which regards the soil as a dynamic complex, continually changing as a result of the climatic processes of weathering together with the effects of vegetation and of the soil flora and fauna, is emphasised throughout. The more detailed elucidation of the relation of soil evolution to the development of vegetation is the most important co-operative task of the immediate future for pedologists and ecologists.

The book is extremely well written, and the exposition perfectly lucid, but parts of it are rather stiff reading for those unfamiliar with the technicalities of modern soil chemistry. It would have appealed to a much wider circle of readers if the author had taken space to amplify and elucidate, as he went along, many of the more abstruse discussions. Prof. Robinson would find that there would be a ready welcome and a good sale awaiting a somewhat smaller book published at a moderate price, omitting the discussions of the more doubtful and difficult points and giving the subject a rather more elementary and less severely concise treatment.

The statement on p. 69 that "in northern coniferous forests there is practically no ground vegetation" can hardly stand. It is only true of close plantations and of dense, relatively young stands; and with that limitation it is almost equally true of most deciduous woods. Mature natural spruce and pine forest may have quite a rich ground vegetation.

The book is a masterly and valuable presentation of a subject on which the knowledge of many of those most intimately concerned is still distressingly vague and even inaccurate.

A. G. T.

THE NOVEMBER ISSUE OF *THE JOURNAL OF ANIMAL ECOLOGY* (VOL. I, NO. 2)

This number contains nine papers, two short notes, a number of short notices of papers on animal ecology, together with some longer reviews and the index for the first volume. F. T. K. Pentelow describes the results of a study of the food of the common trout in the Tees and Itchen, made under the auspices of the Ministry of Agriculture and Fisheries. He finds that almost all food organisms available in the habitat are taken by the fish. This conclusion is also applied in general to West Greenland birds by T. G. Longstaff, in a team-survey of animal and plant communities in Godthaabs Fjord carried out by the Oxford University Greenland Expedition in 1928. This survey gives a clear picture of the whole fauna of an area specially selected for bird census work; there are lists of animals from major habitats, and photographs of some of the latter. D. Ward Cutler, L. M. Crump, and A. Dixon contribute the results of experiments carried out at Rothamsted Experimental Station upon the influence of various environmental factors on Protozoa in sewage filters. R. S. A. Beauchamp, from the Laboratory of the Freshwater Biological Association, describes the behaviour of certain fresh-water flatworms in Blelham Tarn, Westmorland, with reference to their migration and the relationships between different species. The ecology of marine fish receives attention in two papers, one by W. C. Hodgson (from the Fisheries Laboratory at Lowestoft) on the biological and mathematical basis of forecasting changes in the age distribution of herring shoals in the North Sea; the other by B. Storrow (of Cullercoats Marine Biological Station), who discusses the general aims and methods of fishery research, with special reference to forecasting fluctuations in numbers and the relation of these fluctuations to climatic cycles.

The microclimatic conditions of caves and similar places in Palestine are described by P. A. Buxton (London School of Hygiene and Tropical Medicine), who paid special attention to the moisture content of the air, and methods of investigating it in such habitats. Recent changes in numbers and distribution of the American grey squirrel in Great Britain, investigated by the Bureau of Animal Population, Oxford University, are mapped and summarised by A. D. Middleton, who shows that spreading continued during 1930–2 in spite of severe reduction in numbers owing to epidemic disease. The rookeries of the Isle of Wight are mapped and analysed by J. F. Wynne, who agrees with other investigators that the density of the rook population is so low as to have probably little influence on agriculture. Two short notes deal with a periodic fluctuation in wheat-blossom midges (H. F. Barnes), and the orientation of nests of a species of wood-ant which was photographed in North Norway (C. Elton). The number is completed by 131 short notices of British publications on animal ecology; reviews of the August issue of *The Journal of Ecology*, and of books, papers and reports on ornithology, fresh-water fisheries, animal migration, and a nocturnal insect community; and the index for 1932. This second number has been slightly increased in size, and it is intended to expand future issues as the number of subscribers increases.

CHARLES ELTON.

BRITISH ECOLOGICAL SOCIETY

SUMMER MEETING AT BARNARD CASTLE, CO. DURHAM, AUGUST 27TH–31ST, 1932

The summer meeting of the Society was held at Barnard Castle from Saturday, August 27th to Wednesday, August 31st, under the local organisation of Dr R. W. Butcher and Dr T. W. Woodhead. By the courtesy of the Director, Dr E. S. Russell, O.B.E., the Tees Laboratory of the Ministry of Agriculture and Fisheries was placed at the disposal of the Society throughout the meeting, and was utilised as headquarters and meeting place.

On the evening of August 27th at 8.30 p.m. Prof. Boycott took the Chair at the opening of the meeting. Dr R. W. Butcher welcomed the Society on behalf of the Director and Staff of the Laboratory and then gave a concise outline of the geology and topography of Teesdale, as an introduction to the areas to be visited during the meeting. Teesdale was shown to differ greatly in the upper and lower reaches of the river. Above Middleton, from its sources on Cross Fell, the Tees has few tributaries and an average fall of 33 ft. per mile, causing a deep-sided valley liable to big and sudden floods, with a scoured bed and no flood meadow. In this part of its course the Tees is flowing over Mountain Limestone, which consists very largely of sandstones and shales with thin calcareous strata. The water is brown from the peat brought in by tributaries, but has a pH of 6·8–7·4 and contains the characteristic moss of calcareous streams, *Philonotis fontana*. Below Middleton the character of the valley changes where Millstone Grit is brought to the surface by a large synclinal fold. This persists as far as Barnard Castle, below which the surface rock is again Mountain Limestone, and, later, Magnesian Limestone. The geology of Upper Teesdale is complicated by the presence of the Whin Sill. This is a large star-shaped basaltic mass with its centre at Cauldron Snout. It is intruded as a horizontal bed 100–200 ft. thick into the Mountain Limestone. It is responsible for the cascades in the river at High Force and Cauldron Snout, and the limestone into which it has been intruded is metamorphosed at the plane of junction to give the bands of friable crystalline "sugar-limestone" which outcrop on Mickle and Cronkley Fells, and support many of the local subarctic species characteristic of Teesdale. Dr Butcher concluded by referring to the effects upon the district of the most recent glaciation, in which the Pennine and Cheviot glaciers met south of Darlington, depositing thick beds of boulder clay seawards from that town.

Dr K. B. Blackburn then gave an account of the characteristic subalpine species of the Teesdale flora, especially of the region from Winch Bridge (c. 1000′ O.D.) to the highest parts of the neighbouring fells. Descriptions and lantern slides were given of the following species: *Potentilla fruticosa, Arenaria verna, Thlaspi arvense* (on lead workings and tippings), *Viola lutea, Antennaria dioica, Trientalis europaea, Trollius europaeus, Arctostaphylos uva-ursi, Sedum telephium, Vaccinium vitis-idaea, Rubus chamaemorus, Myosotis alpestris, Carex rigida, Gentiana verna, Primula farinosa* (divided by Harrison into coast and upland forms), *Saxifraga stellaris, S. hypnoides, S. aizoides, Bartsia alpina, Sedum villosum, Draba incana, Dryas octopetala, Armeria maritima, Plantago maritima, Helianthemum canum, Senecio spathulifolium, Arenaria uliginosa, Crepis capillaris*. The local distributions of these species were given, frequently related to the Whin Sill basalts or the "sugar-limestone." The central fact of the concurrence of this large number of subarctic species in an "island" distinctly cut off from other areas with similar assemblages, was explained by Dr Blackburn in terms of pre-Glacial survival. According to Dr Raistrick a large nunatak existed in Upper Teesdale

during the most recent glaciation, with smaller ones further south, and the subarctic species are supposed to have survived on these.

Considerable discussion followed the paper, the conclusions of which were strongly disputed. Dr Blackburn's work has been published in *Trans. Northern Naturalists' Union*, **1**, 1931.

The conversazione held on Monday evening was opened at 8.30 p.m. by a series of short descriptions given by the laboratory staff of the work being carried on in the biological investigation of the River Tees. Dr Butcher gave a general introductory statement, and Dr Southgate described the results of domestic and industrial pollution in the estuary, especially upon salmon. Although oxidation of the organic matter in the sewage effluents caused the summer oxygen concentration to fall to 5 per cent. oxygen saturation as against 80 per cent. in winter, yet the April, May and June killing of smolts takes place before the river temperature has risen appreciably, so that the oxygen content is still high. The effect is, in fact, shown to be due to the direct toxicity of cyanides from coke ovens, and water samples can be made innocuous by formaldehyde.

Mr Bassendale described his work and that of his predecessor, Mr Alexander, on the great deficiency in species of the fauna of the middle of the Tees Estuary. This is the region of great variation of salinity, of maximal pollution and toxicity, and of minimal oxygen content. He compared the Tees with the unpolluted Tay, which shows at its estuary the same variation in salinity and also in fauna.

Mr Longland gave an account of the investigation of the decomposition processes undergone by sewage effluents. In the upper Tees there is little yearly variation, but in the lower Tees there is a band of decomposition 15 miles long in winter, but very short in summer. This is indicated especially by the high values of ammonia and nitrates. The seasonal effect is explicable as a temperature effect on the basis of laboratory experiments showing the large measure of control by temperature on the decomposition processes.

A number of exhibits were shown in the laboratory. Mr J. B. Nicholson showed a series of specimens of the rare plants of Teesdale collected between 1830 and 1860. Dr Blackburn exhibited a series of specimens showing variation within populations of *Viola lutea* (agg.) and *Viola tricolor* (agg.) from the county of Northumberland, and also a series showing the variation in the population of an area in which both species occur and hybridise. Dr Woodhead produced a map showing the distribution of rookeries in the Huddersfield district, and also "infra-red" photographs taken in the same region. The photographs showed vegetation on the lower Coal Measures and Millstone Grits, and an extraordinary wealth of detail in the distance, much of which it had not previously been possible to photograph at all.

Dr R. W. Butcher showed maps of permanent quadrats in the bed of the River Tees plotted at intervals from May, 1930 to May, 1932. The most striking points brought out by the quadrats were: (1) the slightness of variation in area occupied by phanerogams through the year, the species concerned being apparently perennial and evergreen, (2) the continued moving of plants to unoccupied areas, (3) that the period of minimal area covered is between February and May. Profile curves of the river bed through the year showed that the plants cause aggregation and stabilisation of mobile substratum in the river bed, the new stratum collected round them consisting of 20 per cent. stones and 70 per cent. sand as compared with 80 per cent. stones and 10 per cent. sand on the rest of the river bed. Dr Butcher also showed photographs and slides of algae found growing on glass slides submerged on the river bed. Many of these are either entirely new or are little known; they have been described in the *New Phytologist*, **31**. A further exhibit by Dr Butcher illustrated the occurrence of six distinct algal communities in the growths on submerged glass slides on the bed of the Tees. In the spring the communities consist of diatoms: (*a*) in the upper river, a *Diatoma*, *Achnanthes*, and *Gomphonema* community, (*b*) in the middle river *Cymbella ventricosa* and *Diatoma* commu-

nities, and (c) in the lower river a *Diatoma, Navicula viridula* and *Surirella* community. In the summer the communities consist of Ulotrichales and a very few diatoms: (a) in the upper river an *Achnanthes, Chaetopeltis* community, (b) in the middle river a *Cocconeis, Chamaesiphonopsis* community, and (c) in the lower river a *Cocconeis, Ulvella, Stigeoclonium* community.

Mr Langland showed figures illustrating the diurnal variation in temperature, oxygen content, *p*H, carbonate and bicarbonate content in the Tees, and also tables showing the range of concentration of decomposition products of sewage in the Tees below the influx of the Darlington sewage.

A third evening meeting was held on Tuesday, August 30th, at 8.30 p.m.

Mr J. B. Nicholson read a paper on the vegetation of Hell Kettles, two large ponds in Lower Teesdale near the confluence of the rivers Skerne and Tees. They were formed by the collapse of the thin New Red Sandstone overlying large cavities formed by solution of the subjacent Magnesian Limestone. The ponds were formed in 1179, and are only 20 ft. deep, despite local belief in a depth compatible with their name. They are 40–50 yards across. One, the single kettle, contains abundant vegetation and shows concentric belts of Phragmitetum, Cladietum and Juncetum obtusiflori. The other pond, the double kettle, is in contrast strikingly barren, probably because of its steep sides and shifting mud. Analyses of the water of the two kettles showed no marked differences; in both the *p*H of the water was 8·3–8·6. Although the content of sodium chloride was not high in either pond, yet several brackish water plants occur beside them, notably *Scirpus tabernaemontani* just above the Cladietum. The general aspect of the vegetation is that of lowland fens such as those of the Norfolk Broads and Wicken Fen, Cambs. Mr Nicholson's work has been described in *The Vasculum*.

Dr F. T. K. Pentelow then described the ecology of the distribution of the larvae of some species of *Scinidium* in the River Tees. The larvae of seven species of this small black blood-sucking fly occur in the Tees, four species throughout its entire length. At the confluence of the River Skerne *S. reptans* var. *galeratum* comes in and extends downwards. *S. equinum* is abundant also in the Lower Tees. The Skerne differs completely from the Tees, and contains *S. reptans, S. ornatum* and *S. aureum*. The Skerne is heavily polluted with the Darlington sewage and the water is hard. Below the confluence the Skerne water produces in the Tees biological effects closely approximating to those of stagnant water. This seems certainly due to the sewage rather than to the hardness, but the effect possibly operates through the very greatly increased abundance of flowering plants in the river below the Skerne confluence.

The meeting was concluded by the President, Prof. Boycott, expressing the deep gratitude of the meeting and of the Society to the local organisers, Dr Butcher and Dr Woodhead, to the Staff of the Laboratory and their wives and friends and all who had co-operated to make the meetings and excursions so successful and enjoyable.

During the meeting three excursions were made, all of them in the competent charge of Dr Butcher.

On Sunday, August 28th, the party travelled by bus to Langdon Beck and from there walked over Widdybank Fell to Cauldron Snout, visiting High Force after tea, and Winch Bridge on the return journey to Barnard Castle. By the farm near Langdon Beck were found *Peucedanum ostruthium* and *Rumex domesticus*, the latter locally used as a horse medicine. On the morainic slopes of Widdybank Fell a wide complex of grazed communities was traversed, dominated variously by *Nardus stricta, Molinia coerulea, Juncus effusus*, Carices and *Eriophorum*. It appeared that soil factors, such as soil reaction and mineral content and local drainage, the intensity and character of grazing, and past cultivation were all factors heavily involved in differentiating the complex of communities, and Dr Woodhead showed that it was probable that all these operated after tree-felling had cleared the original woodland. In the alkaline drainage channels crossing the otherwise acid soil of the fell were found

Tofieldia palustris, Saxifraga aizoides, Kobresia caricina, Bartsia alpina, Eriophorum lati-folium, and *Primula farinosa. Sedum villosum* was discovered growing in very disturbed ground such as cart-ruts and hoof-marks, especially in some wet places. On the "sugar-limestone" of Widdybank Fell were found *Antennaria dioica* and *Arenaria verna*. On the basalt of the Whin Sill at High Force and Winch Bridge were *Potentilla fruticosa, Saussurea alpina, Galium boreale, Rubus saxatile, Melampyrum silvaticum, Antennaria dioica* and *Kobresia caricina.*

On Monday the party walked down the rocky limestone gorge of the Tees to Rokeby. On the way Dr Butcher demonstrated his technique for investigating the algal flora of rivers by the use of submerged metal frames containing glass microscope slides. The algae developing on the slides are quite typical of those covering the stones of the river bed and are also the main source of the river plankton. *Ribes alpinum* and *Daphne laureola* both occurred in the valley.

On Tuesday, August 30th, the excursion was by bus to Grains o' Beck, and thence on foot over Mickle Fell and Cronkley Scars to Langdon Beck, returning by bus to Barnard Castle. On the slopes of the fell *Epilobium alsinifolium, Philonotis fontana* and *Saxifraga stellaris* occurred rather strikingly in alkaline flushes in the acid peat. At the summit of Mickle Fell and again on Cronkley Scars the outcrop of limestone bands among sandstone and shales of the Mountain Limestone produced the most striking and instant change from vegetation dominated by *Calluna, Eriophorum* and *Juncus squarrosus,* to bright green, closely grazed grassland of definite calcareous type with *Festuca ovina* as the main component. On Mickle Fell these areas bore also *Gentiana verna* and *Draba incana*. The upper parts of Mickle Fell showed magnificent examples of peat degeneration, the erosion channels often reaching the basal rock: in the Fish Lake at Amgill Beck the basal peat showed the stumps (mostly *Betula*) of former woodland. The "sugar-limestone" outcrop on Cronkley Scars showed *Dryas octopetala, Gentiana verna, Arenaria verna* and *Helianthemum canum.*

Of the large number of Teesdale rarities seen during the excursions it was marked that so many occurred in situations characterised by soil alkalinity: the basalt of the Whin Sill, the alkaline fell flushes, the limestone outcrops and the "sugar-limestone." In some cases, such especially as the "sugar-limestone" and the basalt, one might suppose the alkalinity to be linked with excellent drainage. It is still by no means clear how the influence of such edaphic factors interrelates with the "nunatak hypothesis" of the survival of the Teesdale flora throughout the Glacial period.

MEETING AT UNIVERSITY COLLEGE, LONDON, JANUARY 6TH–7TH, 1933

SOIRÉE IN THE DEPARTMENT OF BOTANY

The members of the Society and visitors were entertained at a Soirée kindly arranged by Prof. E. J. Salisbury in the Botanical Department on the evening of Friday, January 6th. A large number of members and guests were present. Several series of exhibits had been arranged in the laboratories. Some of the more striking features of Molluscan distribution in Britain which were referred to in the Presidential address on the following day, were here illustrated by maps and specimens of the animals concerned. Other Molluscan exhibits by the President showed the wide range of naturally occurring forms of *Limnaea peregra,* and the equally wide range produced by breeding. Mr A. D. Cotton showed a selection of dried specimens of arborescent Senecios which are found on the high equatorial mountains of Africa. The species are peculiar to each mountain mass and occur in zones from about 9000 to

14,000 ft. The plants are characterised by a short woody trunk bearing terminal rosettes of very large leaves, which in the upper species are covered on the under side by a dense tomentum. In the two lowermost zones the capitula are heterogamous, but in some species of the uppermost zone they are homogamous (devoid of ray florets). An exhibit of drawings and microscope slides by Mr C. L. Hare showed the general features of the anatomy of the arborescent Senecios described by Dr Cotton. Mr C. E. Hubbard showed living and herbarium specimens of *Entolasia subjuncea* and other cleistogamous grasses: in some cases these were produced on the ends of short underground shoots. Mr A. D. Middleton showed specimens of young forest trees very severely injured by the attacks of field voles (*Microtus hirtus*). He also showed a trap for catching field voles alive in surface runs among ground vegetation: the trap incorporates a nest-box, since the voles die within a few hours if kept in conventional traps. Mr F. W. Jane illustrated by sections and diagrams of the wood of different species of the genus *Celtis* the tendency of the abundance of vessels in the secondary wood to vary with the latitude. In the twenty-six species examined it seemed, broadly speaking, that the tropical species had a smaller area of the transverse section occupied by vessels than species from more temperate regions. Prof. E. J. Salisbury showed a series of charts and photographs illustrating altitudinal zonation in *Quercetum sessiliflorae*. The zones of Vaccinietum, Luzuletum and Anemonetum which occupy summit, upper and basal slopes respectively, showed marked gradation also in respect of the soil factors of carbonate content, exchangeable calcium, soil reaction and non-available water. Prof. Salisbury also showed photographs of vivipary in *Salicornia herbacea* and lantern slides of several rare species of British flowering plants. Exhibits from the work of the Department carried out at Blakeney Point included charts showing the soil and air temperatures and the water content of sand-dunes, and drawings to scale of the root systems of littoral plant species. The latter strikingly illustrated the great plasticity of the root system produced according to the character of the ground occupied.

ANNUAL MEETING

The nineteenth Annual Meeting of the Society was held in the Department of Botany of University College on the following morning, Saturday, January 7th, at 10 a.m., the President, Prof. A. E. Boycott, F.R.S., occupying the Chair. The minutes of the previous meeting were read and confirmed, and the Secretary's report on the activities of the Society during the past year was read and adopted.

HON. SECRETARY'S REPORT FOR THE YEAR 1932

The eighteenth Annual Meeting of the Society was held in the Departments of Botany and Zoology of the University of Oxford on January 2nd and 3rd, 1932. On the evening of January 1st members of the Society and guests were entertained at a Soirée in the Department of Zoology and Comparative Anatomy, Oxford, at which numerous exhibits were shown dealing with aspects of animal ecology. The cordial thanks of the Society are due to the heads and staffs of the two departments for their generous hospitality.

The summer meeting of the Society was held in Teesdale from August 27th to 31st, and by courtesy of the director and staff the Tees Laboratory of the Ministry of Agriculture and Fisheries at Barnard Castle was made available as headquarters and meeting place. Two evening meetings were held at which papers were communicated dealing with the local ecological features, and at a Soirée kindly given by the staff of the laboratory the work of the Station was outlined by means of short talks and prepared exhibits. Other exhibits of more general ecological interest were also shown. During the meeting two whole day excursions and one half-day excursion were made into Upper Teesdale. The party walked over Cronkley, Widdybank, and Mickle Fells, and visited Cauldron Snout, High Force, and Winch Bridge,

seeing a very large part of the characteristic local subarctic flora of Teesdale and a wide range of typical moorland vegetation. The society is very grateful to the local organisers, Drs Woodhead and Butcher, and to the Staff and Director of the Tees Laboratory for having made the meeting so successful and pleasant.

On Saturday, October 22nd, a joint excursion with the British Mycological Society was made at Albury, under the leadership of Mr J. Ramsbottom.

At the last Annual Meeting it was agreed that the Council of the Society be confirmed in its decision to proceed with the publication of a new *Journal of Animal Ecology* under the editorship of Mr C. S. Elton, with Mr A. D. Middleton as assistant editor. During the year two numbers of the new *Journal* have been produced, appearing in May and November, and containing respectively 100 and 114 pages. The volume included 17 original papers, reviews, notes and notices of publications bearing on animal ecology, and the illustrations included nine plates.

In spite of prevailing economic conditions there has been a very favourable response to the publication of the new *Journal*: at the end of 1932 51 members of the Society are taking both *The Journal of Ecology* and *The Journal of Animal Ecology*, 62 are taking *The Journal of Animal Ecology* only, a total of 113 copies distributed to members (*Journal of Ecology*, 243). Direct sales by the publishers to non-members amount to over 70. The Society is grateful to the Royal Society for a further grant of £100 towards the cost of launching the new *Journal*.

During the past year two numbers of *The Journal of Ecology* have been issued containing together 432 pages, supplements of 32 pages and 29 plates. A general index to the first 20 volumes of the *Journal* with a full citation of subjects is now in preparation and will be issued during the spring of 1933. (See separate leaflet enclosed in this issue.)

The Society's transplant experiments at Potterne are continuing satisfactorily under the control of Mr Marsden-Jones and Dr Turrill; a second report of their progress will appear in the second number of *The Journal of Ecology* for 1933. The thanks of the Society are due to the British Association for a grant of £5 in aid of these experiments.

The Society has accepted from Mr W. B. Crump the generous gift of a collection of photographic negatives of British vegetation: from these lantern slides and prints will eventually be available for the use of members.

Since the end of last year the membership has risen from 242 to 305. Sixty-nine new members have been elected and six members have resigned. Of the new members five are receiving *The Journal of Ecology* alone, 49 *The Journal of Animal Ecology* alone and 15 are receiving both *Journals*. Eight old members have transferred from *The Journal of Ecology* to *The Journal of Animal Ecology*. Thirty-six old members of the society receive the new *Journal* as well as continuing with *The Journal of Ecology*.

We regret to record the resignation of Prof. O. V. Darbishire, one of the original founders of the Society.   H. GODWIN.

The meeting proceeded to the election of officers as follows:

Vice-President: Dr A. J. WILMOTT (retiring Prof. J. R. MATTHEWS).

Council members: Mr C. OLDHAM, Dr W. B. TURRILL (retiring Mr O. W. RICHARDS, Mr V. S. SUMMERHAYES).

Hon. Editor of The Journal of Ecology: Prof. A. G. TANSLEY.

Hon. Secretary: Dr H. GODWIN.

The President having explained that under existing rules the Editor of *The Journal of Animal Ecology* was not an *ex-officio* member of the Council, it was agreed that the rules be amended to give him this status, the size of the Council being correspondingly increased by one.

The amended rules as agreed to are:

9. The Society is governed by a Council of *fifteen* Members, including the President, two Vice-Presidents, *two* Hon. Editors, the Hon. Secretary and the Hon. Treasurer of the Society.

11. The Officers of the Society are the President, two Vice-Presidents, the Hon. Treasurer, the *two* Hon. Editors and the Hon. Secretary. The President and two Vice-Presidents shall be nominated from among existing Members of the Council. The *two* Hon. Editors and the Hon. Secretary retire at the end of each year, but are eligible for re-election.

16*a*. The *two* Hon. Editors *are ex-officio* Members of the Council.

The vacancies in the Council caused by this change of rules were then filled as follows:

Hon. Editor of The Journal of Animal Ecology: Mr C. S. ELTON.

Council Member: Dr T. W. WOODHEAD.

The President then delivered his address on "Mollusca and Man in Britain." On the proposition of Prof. Tansley a unanimous vote of thanks was given to the President for his extremely interesting address.

Mr A. D. Cotton gave an account of the ecological conditions under which the tree Senecios of the African tropical mountains occur. All are water-loving species, but having an altitudinal range of 5000 ft. they are found under widely varying conditions. The lowermost species with thin leaves are found at the uppermost limit of the rain forest. In the subalpine zone (or mountain meadow) where there is exposure to sun and wind, one or more species occur whose leaves are more or less protected on the under side by a tomentum. The most striking species are those of the high alpine zone (12,000–14,000 ft.), which extend to the limit of the phanerogamic vegetation. Here hot sun by day alternates with severe frost at night, and cloud, rain, and hail alternate with drying winds. The leaves of the uppermost species are thick, very large, and protected by a very thick tomentum and possess very copious oil vessels.

Dr C. L. Hare spoke briefly of the morphological features shown on preliminary investigation of the anatomy of some of the species referred to by Mr Cotton. They illustrated a rather striking combination of xeromorphic and hygromorphic features corresponding with the general character of their natural environment.

After the adjournment for lunch the accounts for the year (see p. 227) were presented by the Treasurer and were adopted. It was proposed and carried that Messrs William Norman and Sons be reappointed Auditors to the Society, and a very hearty vote of thanks was given to Mr Boyd Watt for his care and skill in handling the finances of the Society.

Prof. T. A. Stephenson gave an account of initial investigations of the marine ecology of the Cape Peninsula, pointing out how the interaction of the warm Agulhas current and the cold Benguella current was apparently a major factor influencing littoral life, both animal and plant. This was illustrated by records of the physical conditions round the coast and of the difference in behaviour shown by *Ecklonia, Caulerpa* and other organisms under the influence of the two different currents. Results of the investigations of the biological and physical conditions of rock pools in the area were also given.

Mr D. Lack then read a paper on habitat preferences of birds. During an investigation of bird distribution on the Breckland, particularly with regard to the changes due to the recent afforestation, it was found that birds were limited not only by their essential requirements, food, nesting sites, etc., but by the presence of certain conspicuous features of the habitat, such as a tree in the case of the tree pipit, which could not be correlated with any essential requirements. The demand for these could only be psychological, these features being the recognition marks of the habitat of the species concerned. Though these limitations might on occasion be successfully broken through, they were normally adhered to with great constancy.

ᴵ Prof. R. S. Adamson then described the vegetation of Robben Island, Table Bay, South Africa. Rabbits had been introduced there about a hundred years ago, although they were still not present on the mainland, and the island vegetation (which had not been much influenced by man) showed very considerable contrast with the natural vegetation of the mainland. Primary features of difference were the absence of shrubs which are dominant on the mainland and the peculiar open plant communities which under rabbit pressure have replaced them. Annuals make up a large part of the population, the few perennials being highly rabbit resistant. The rabbits exist through the dry season by feeding on the succulent leaves of a recently introduced shrub, *Miaponum*.

Dr H. Godwin read a paper by himself and Mr J. S. Turner on soil acidity and vegetational succession at Calthorpe Broad, Norfolk. The vegetational succession from reed-swamp and fen, through carr to woodland, was shown to give a concentric zonation round the broad with a soil-level increasingly higher above water-level, and a soil reaction increasingly acid from the broad outwards. The high soil acidities were correlated with the occurrence of acidiphilous species, and were attributed to the natural processes of soil development. The relation of such progressive soil acidification to climax vegetation was discussed, and it was suggested that although "Hochmoor" certainly formed the climax in many parts of the west of England, in the east the evidence pointed rather to a deciduous forest climax of the mixed oak-wood type.

The meeting adjourned for the tea provided by the generosity of the Botanical Department, and the meeting was closed by according a very hearty vote of thanks to Prof. Salisbury and his Staff for their liberal hospitality.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR YEAR ENDING 31ST DECEMBER, 1932

Income

	£	s.	d.	£	s.	d.
Subscriptions received including arrears	351	4	4			
less prepayments for 1933	17	7	4	333	17	0
Interest on Investments				42	10	0
Interest on Deposit Account				1	17	7
Bonus on Conversion of War Loan (5% to 3½%)				7	0	0
Income Tax refunded (for 1930-31 and 1931-32)				4	4	5
Journal of Ecology—Sales, etc.:						
Current volume xx, 1932	471	5	0			
Back volumes and parts	124	15	9			
Advertisements				596	1	0
Journal of Animal Ecology, volume 1, 1932:						
Subscriptions received	129	17	6			
Grant from Royal Society, in 1931	100	0	0			
Sales	101	7	1	331	4	7
				£1316	14	7

Expenditure

	£	s.	d.	£	s.	d.
Working Expenses:						
Printing Circulars, etc.	6	13	3			
Postages, etc.	15	7	7			
Bank Charges	1	7	1			
Clerical Assistance (Secretary and Treasurer)	15	0	0	38	7	11
Audit Fee				3	3	0
Fresh Water Biological Association of the British Empire—Grant in aid				10	0	0
British Ecological Society's Transplant Com. Fund—Donation				5	0	0
Soirée Expenses				2	5	0
Journal of Ecology:						
Paper, Printing, Illustration, etc.	663	12	4			
Binding	3	2	3			
Postage, etc.	38	6	5			
Insurance of Stock	2	5	2			
Publishers' Commission	84	1	1			
Back parts purchased	32	17	6	824	4	9
Journal of Animal Ecology:						
Paper, Printing, Illustration, etc.	297	15	5			
Publishers Commission	20	11	9			
Carriage, Insurance, Advertising, etc.	15	8	11	333	16	1
				1216	16	9
Balance—Surplus for the Year				99	17	10
				£1316	14	7

BALANCE SHEET AT 31ST DECEMBER, 1932.

Liabilities

	£	s.	d.	£	s.	d.
Membership subscriptions, prepaid for 1933				17	2	4
Membership subscription overpaid, to refund				1	0	0
Journal of Animal Ecology:						
Prepaid Subscriptions for 1933				3	0	0
Grant from Royal Society, 1932				100	0	0
General Revenue Account—Balance of Funds:						
Surplus at 31st December, 1931	890	2	10			
add Balance from Revenue Account	99	17	10	990	0	8
				£1316	14	7

Assets

	£	s.	d.	£	s.	d.
Westminster Bank—Credit Balances:						
Current Account	95	15	0			
Deposit Account	100	0	0	195	15	0
Investments:						
£700 3½% War Loan at cost (Market value at 31st December, 1932, at 98¾, £691. 5s. 0d.)	717	3	0			
£200 5% Conversion Loan at cost (Market value at 31st December, 1932, at 115¼, £230. 10s. 0d.)	198	10	0	915	13	0

Note. A further asset is the unsold stock of the *Journals* held for the Society by the Publishers.

Audited and found correct and as shown by the Account Books of the Society. The items of Bank Balance and Investments have been verified by Bank Certificates.

(signed) WM. NORMAN & SONS.
Chartered Accountants.

LIST OF MEMBERS (January, 1933)

E. = Takes *The Journal of Ecology.* A. = Takes *The Journal of Animal Ecology.*

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary,* Dr H. Godwin, Botany School, Cambridge.

E. A. **Adams**, C. C.; New York State Museum, Albany, New York, U.S.A.
E.   **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
E.   **Allan**, Dr H. H.; Plant Research Institute, Palmerston North, N.Z.
E. A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
  A. **Alexander**, W. B., M.A.; University Museum. Oxford.
E.   **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E.   **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E.   **Andersonian Naturalists' Society** (cf. Glasgow).
E.   **Andreánszky**, Baron Gábor; Budapest, VIII, Múzeûm-Körur 4, Hungary.
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
E.   **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
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E.   **Bharucha**, F. R.; Collège des Écossais, Plan des Quatre Seigneurs, Montpelier, France.
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E. **Eden**, T.; Tea Research Institute, St Coombs, Talawakelle, Ceylon.

E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.

E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.

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　　A.　**Gilbert**, H. A., B.A.; Bishopstone, Hereford.

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BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

(1) CANADA (COLLABORATOR, J. E. DANDY)

713. Linder, D. H. "Brief Notes on the Helicosporeae with Descriptions of Four New Species." *Ann. Missouri Bot. Gard.* **18**, pp. 9–16. Figs. 1–2, Plate 2 (erroneously numbered 1). 1931. (1. 176.)

In these notes on Helicosporeae (Fungi Imperfecti) the author reports *Helicosporium griseum* from North America for the first time, one of the specimens being from Canada (Toronto). *Helicoma ambiens* is recorded from London, Ontario, whilst *H. olivaceum* and *Helicoon ellipticum* are both reported from Winnipeg.

714. Roush, Eva M. F. "A Monograph of the Genus *Sidalcea*." *Ann. Missouri Bot. Gard.* **18**, pp. 117–244, Figs. 1–3, Plates 5–13. 1931. (1. 177.)

The genus *Sidalcea* (Malvaceae), according to this monograph, is represented in Canada by a single species, *S. Hendersonii*, which extends northwards from Oregon and Washington into British Columbia, where it is found in the south of Vancouver Island and on the adjacent mainland. *S. Hendersonii* belongs to the section *Perennes* of subgenus *Eusidalcea*.

715. Rydberg, P. A. "Notes on Fabaceae—XIII." *Bull. Torr. Bot. Club,* **57**, pp. 397–407. 1931. (1. 178.)

In this contribution Rydberg deals with the North American species of the genus *Tium*, a segregate from *Astragalus*. The only Canadian species is *T. Drummondii* (sect. *Racemosa*), which is distributed from Saskatchewan and Alberta southwards into the United States.

716. Anderson, W. B. "A *Sisyrinchium* New to Canada." *Gard. Chron.* Ser. 3, **89**, p. 219. 1931. (1. 179.)

Olsynium (Sisyrinchium) inflatum (Iridaceae) is recorded from Canada for the first time. It was collected by the author in the vicinity of Adams Lake, south-eastern British Columbia. Previously the species was known from Washington and northern Idaho.

717. Perry, Lily M. "Contributions from the Gray Herbarium of Harvard University—No. XCIV. The Vascular Flora of St. Paul Island, Nova Scotia." *Rhodora,* **33**, pp. 105–126, Map. 1931. (1. 180.)

St Paul Island, which lies about 12 miles north-east of Cape North, Nova Scotia, is one of the smaller islands of the Gulf of St Lawrence. It is well known that at least portions of the Magdalens, Anticosti, and the Mingans, other islands in the Gulf at some distance from the mainland, escaped the Pleistocene denudation and consequently have been of particular interest phytogeographically. Presumably St Paul also was far enough from the

mainland to continue unglaciated, except perhaps locally, and thus its flora too might offer some interesting relics. This possibility and the smallness of the island induced the author and Dr Muriel V. Roscoe to spend a month's vacation there during the summer of 1929 collecting botanical specimens. It was their aim to make a complete collection of the vascular flora of St Paul, but unfortunately they were unable to reach a small part of the island, Mica Head. In spite of this lacuna, however, the collection made was fairly representative of the flora of St Paul; it included about 2360 sheets of specimens, in all 418 numbers embracing 160 genera and approximately 300 species and varieties. These, in large part, are common to the flora of Nova Scotia; some are found only in Cape Breton Island and St Paul, while others—20 in all—were collected in the province for the first time and most of them illustrate definite range-extensions from the north. It is significant that these northern plants are characteristic of slightly or not at all glaciated regions in Newfoundland, Quebec, Anticosti, or the Magdalens; hence, if a parallel conclusion may be drawn, it seems not unreasonable to infer that St Paul also escaped denudation by the Wisconsin ice-sheet.

The first part of Miss Perry's paper consists of an account of the island (with map) and of the trip, with some description of the vegetation met with and mention of many of the more interesting plants. The remaining part takes the form of a systematic list of the vascular plants collected. In this list the twenty plants recorded for the first time from Nova Scotia are marked with asterisks, and are as follows:

Deschampsia flexuosa var. *montana*, *Festuca rubra* var. *arenaria*, *Agropyron caninum* var. *Hornemannii*, *Carex gynocrates*, *C. crinita* var. *simulans*, *Luzula campestris* var. *comosa*, *Salix Uva-ursi*, *S. cordifolia* var. *callicarpaea*, *Geocaulon lividum*, *Silene acaulis* var. *exscapa*, × *Pyrus Arsenei*, *Amelanchier Fernaldii*, *Sanguisorba canadensis* var. *latifolia*, *Oxytropis johannensis*, *Cornus suecica*, *Vaccinium Oxycoccus* var. *intermedium*, *Rhinanthus groenlandicus*, *Utricularia ochroleuca*, *Campanula rotundifolia* var. *alaskana*, and *Solidago multiradiata*.

718. Roscoe, Muriel V. "The Algae of St. Paul Island." *Rhodora*, **33**, pp. 127–131, Figs. 1–2. 1931. (1. 181.)

This paper gives an account of the algae collected by the author in St Paul Island during the same expedition as that dealt with in Abstract **717**. The collection does not necessarily represent an inclusive list of the marine algae of the island, though, since the accessible regions were also in the most protected areas, it is felt probable that few forms escaped detection. The only fresh-water forms collected belong to the genus *Batrachospermum*, and the abundance of *B. vagum* in Ethel Lake, where it formed a dense growth over the rocks in shallow water, calls for special comment; a second species, *B. moniliforme*, was discovered in the streamlet draining into Kay Cove.

A list is given of thirty-nine species and varieties which have been identified.

719. Juel, H. O. "The French Apothecary's Plants in Burser's Herbarium." *Rhodora*, **33**, pp. 177–179. 1931. (1. 182.)

The author publishes an enumeration of the North American plants preserved in Burser's *hortus siccus*, which is in the Botanical Museum at Upsala. C. Bauhin, in his *Prodromus Theatri botanici* (1620), described several plants which had been communicated to him by Burser who had received them from an unnamed apothecary in Paris, with the statement that they were collected in the country named Toupinambault in Brazil. Specimens of these plants, in addition to a few others from the same source, are inserted in Burser's *hortus siccus*. On his labels the same statement is given about their origin, with the exception of one plant (*Trillium*) which is said to be from "Gallia nova," that is, the colony

"Nouvelle France" which the French had founded on the St Lawrence River about the year 1608. Since, however, all the plants belong to North American species it may be assumed that they were all collected in Canada. Linnaeus, who made extensive studies in Burser's *hortus siccus*, came to the same conclusion about the origin of these plants.

720. Fernald, M. L. "*Potentilla canadensis* and *P. simplex.*" *Rhodora*, **33**, pp. 180–191, Plates 214–215. 1931. (1. 183.)

The nomenclature of two North American species of *Potentilla* (Rosaceae) is here readjusted. Linnaeus's name *P. canadensis* should replace *P. pumila*, whilst the species which has been treated as *P. canadensis* in recent literature should be called *P. simplex*. The two species concerned both belong to the Canadian flora. Fernald fully revises them, and according to his treatment *P. canadensis* is represented in Canada by the typical variety (var. *typica*), which extends into south-eastern Ontario from the eastern United States. *P. simplex* is represented in Canada by two varieties: var. *typica*, which inhabits south-eastern Canada and the eastern United States, and var. *calvescens* (a new variety), which ranges from Newfoundland and south-eastern Canada into the eastern United States.

721. Fernald, M. L. "*Pedicularis labradorica.*" *Rhodora*, **33**, p. 193. 1931. (1. 184.)

The North American Scrophulariaceous plant which is generally known as *Pedicularis euphrasioides* should be called by the earlier name *P. labradorica*, published by Houttuyn.

722. Kennedy, R. B. "Further Notes from Southwestern Newfoundland." *Rhodora*, **33**, pp. 207–209, Plates 216–217. 1931. (1. 185.)

This comprises notes on plants collected by the author from June 1st to September 15th, 1930, along some of the salmon streams of south-western Newfoundland. *Lonicera villosa* var. *tonsa*, *Aster paniculatus*, *Festuca longifolia*, and *Ranunculus Gmelinii* are recorded from Newfoundland for the first time, while *Rubus Kennedyanus* and *R. pergratus* var. *terrae-novae* are described and figured as new by M. L. Fernald.

723. Fernald, M. L. "*Potamogeton tenuifolius* Raf." *Rhodora*, **33**, pp. 209–211. 1931. (1. 186.)

Fernald takes up the earlier name *Potamogeton tenuifolius* in place of *P. microstachys*, and proposes the new combination *P. tenuifolius* var. *subellipticus* based on *P. microstachys* var. *subellipticus*. See Abstract **487**.

724. Porsild, M. P. "On the 'Papillose' Achenes in the Genus *Antennaria.*" *Rhodora*, **33**, pp. 213–222, Figs. 1–4. 1931. (1. 187.)

The occurrence and taxonomic importance of "papillae" or achenial hairs on the achenes of species (including Canadian representatives) of *Antennaria* (Compositae) are discussed. Examples of the "papillae" are described and figured.

725. Fernald, M. L. and **Weatherby, C. A.** "Some New Plants from the Gaspé Peninsula." *Rhodora*, **33**, pp. 231–240, Fig. 1. 1931. (1. 188.)

In this paper the authors give notes on some of the plants collected while botanising in Gaspé County, Quebec, both on Mt St Pierre and on the more available talus slopes and cliffs from near Rivière à la Martre to Gros Morne. The trip took place in early July, 1931. *Carex clivicola*, *Saxifraga cernua* var. *latibracteata* (which occurs also in Baffin Island,

Keewatin, and Alberta), *Rubus idaeus* var. *eucyclus*, and *Astragalus scrupulicola* are described as new. *Amelanchier sanguinea* var. *gaspensis* is raised to the rank of a species under the name *A. gaspensis*; it is confined to the Gaspé Peninsula and neighbouring parts of Quebec.

726. Raup, H. M. "*Salix glauca* and its Allies in the Athabasca-Great Slave Lake Region." *Rhodora*, **33**, pp. 241–244, Plate 218. 1931. (1. 189.)

A large number of specimens of *Salix glauca* and its close relatives were collected in good fruiting condition by the author in the Athabasca-Great Slave Lake region during recent summers. The greater part of these fall definitely into one group and appear to be inseparable from the European *S. glauca*, but three other groups are rather clearly segregated. Typical *S. glauca*, of wide range in Europe and North America, is confined to rich woods or the muskeg borders of lakes and streams. Most of the specimens of it are from the gently rolling upland west of the upper Slave River. *S. glauca* var. *acutifolia*, a well-marked form with a wide-ranging consistency in Alaska and the northern Cordilleran region, is confined to the rocky uplands of the pre-Cambrian country east of the Slave River district; it has a range somewhat similar to that of another willow common in Alaska and entering the Great Slave Lake basin, namely *S. alaxensis*. Although the *acutifolia* group is confined to the semi-barren rocky country, typical *S. glauca* grows in the least exposed and richest woods at the eastern end of Great Slave Lake. *S. desertorum* was collected on the bleak exposed rocky shores on the north side of McLeod Bay, Great Slave Lake, while *S. brachycarpa* var. *antimima* (a new combination based on *S. chlorolepis* var. *antimima*) was seen only in the semi-open prairies and on the upper slopes of the Caribou Mountains west of the Slave River. *S. desertorum*, however, may prove to be nothing more than an occasional dwarfed form of the woodland *S. glauca*. Its rarity is attested by its sporadic occurrence in herbaria, although the regions in which it grows have yielded several other species of willows. It should also be noted that it has never been found in the extreme arctic regions, but only in districts near or in contact with wooded areas where *S. glauca* occurs.

727. Victorin, M. "*L'Anacharis canadensis*." *Contrib. Lab. Bot. Univ. Montréal*, **18**, pp. 1–43, Figs. 1–7. 1931. (1. 190.)

In this contribution Victorin outlines and thoroughly discusses the confusion which has surrounded the taxonomy and nomenclature of *Elodea canadensis* (Hydrocharitaceae), a species which was originally described from the vicinity of Montreal. He concludes that this plant of south-eastern Canada should be referred to the genus *Anacharis* under the name *A. canadensis*, and that the western form (occurring in Saskatchewan) which has been known as *E. Planchonii* should be considered a variety of the same species, with the name *A. canadensis* var. *Planchonii* (a new combination). The paper is in French.

728. Rousseau, J. "Études floristiques sur la région de Matapédia (Québec)." *Mus. Nation. Can. Bull.* **66**, pp. 1–25, Fig. 1, Plates 1–2 A. 1931. (1. 191.)

In the summer of 1929 the author spent six weeks in botanical exploration of a region of Quebec adjacent to the Restigouche County of New Brunswick. The area studied lies in the Matane, Bonaventure, and Rimouski Counties of Quebec, and includes the valleys of the Matapedia and Patapedia Rivers with the intervening portion of the Restigouche. The species collected are set out in an annotated list; they include a new forma, *Equisetum arvense* var. *boreale* f. *caespitosum* (Equisetaceae), and a new hybrid, *Anemone multifida* var. *hudsoniana* × *riparia* (Ranunculaceae). The paper, which is in French, includes a map of the region dealt with.

729. Rousseau, J. "Notes sur la flore de la région de Saint-Urbain, Comté de Charlevoix (Québec)." *Mus. Nation. Can. Bull.* **66**, pp. 26–30, Figs. 2–3, Plate 2 B. 1931. (1. 192.)

During the first week of July, 1929, the flora of the region of St Urbain (Charlevoix County, Quebec) was studied, particularly that of the Montagne du Lac des Cygnes and the Montagne des Ilets. Notes are given on the most characteristic species. *Larix laricina* f. *depressa* (Pinaceae) is described as new; it occurs also in other parts of Quebec and in Newfoundland. The most interesting plant is considered to be *Carex capitata* (Cyperaceae), and a map is given showing the distribution of this sedge in North America. Another map illustrates the region visited. The paper is in French.

730. Pugsley, H. W. "A New *Juncus* in Scotland." *Journ. of Bot.* **69**, pp. 278–284, 1 Fig. 1931. (1. 193.)

Juñcus Marshallii (Juncaceae) is described and figured as a new species. The type is from Scotland, but the species is said to occur also in Newfoundland.

731. Dowding, Eleanor S. "Floral Morphology of *Arceuthobium americanum*." *Bot. Gaz.* **91**, pp. 42–54, Figs. 1–11. 1931. (1. 194.)

An account of the floral morphology of the parasitic phanerogam *Arceuthobium americanum* (Loranthaceae), which infects the soft pines in Canada and the United States. The ecology of this parasite in central Alberta was dealt with by the same author in 1929. See Abstract **388**.

732. Atkinson, G. F. "Notes on the Genus *Lemanea* in North America." *Bot. Gaz.* **92**, pp. 225–242. 1931. (1. 195.)

Lemanea (Lemaneaceae) is a genus of fresh-water Rhodophyceae. The only Canadian form dealt with in this paper is *L. fucina* var. *rigida*, which belongs to the section *Sacheria* and is widely distributed in North America; material of it is cited from Ontario, New Brunswick, Newfoundland, Nova Scotia, and British Columbia (Vancouver Island).

733. Haddow, W. R. "Studies in *Ganoderma*." *Journ. Arnold Arb.* **12**, pp. 25–46, 1 Fig., Plates 29–30. 1931. (1. 196.)

This includes a review of the taxonomic history of the genus *Ganoderma* (Polyporaceae) and an account of studies on four of its species. Of the species studied three are found in Canada; these are *G. oregonense*, *G. lucidum*, and *G. sessile*.

734. Palmer, E. J. "Conspectus of the Genus *Amorpha*." *Journ. Arnold Arb.* **12**, pp. 157–198, 2 Figs., Plate 36. 1931. (1. 197.)

A revision of the genus *Amorpha* (Leguminosae), with a key to the species, varieties, and formae. Three of the species are represented in Canada: *A. canescens* (typical), *A. nana*, and *A. fruticosa* (var. *angustifolia*).

735. Cummins, G. B. "*Phragmidium* Species of North America: Differential Teliospore and Aecial Characters." *Mycologia*, **23**, pp. 433–445, Plate 32. 1931. (1. 198.)

Nineteen North American species of *Phragmidium* (Pucciniaceae) are recognised. The paper includes two keys to these species, one based on aecial characters, the other on teliospore characters.

736. Koch, L. W. "Spur Blight of Raspberries in Ontario caused by *Didymella applanata*." *Phytopathology*, **21**, pp. 247–287, Figs. 1–11. 1931. (1. 199.)

"Spur blight" (often referred to also as "cane blight") is a fungous disease of raspberries, caused by *Didymella applanata* (Sphaeriaceae). It is prevalent in the Niagara Peninsula and is gradually becoming a problem of importance to the growers of that district.

737. Atwell, E. A. "Occurrence of *Cadophora fastigiata* in Canada." *Phytopathology*, **21**, p. 761. 1931. (1. 200.)

Cadophora fastigiata, a recently described fungus, is reported from Canada. It was isolated by the author from stained sapwood obtained in Canada from the following species: *Picea canadensis*, *Pinus strobus*, *P. Banksiana*, and *Pseudotsuga taxifolia*.

738. Brinkman, A. H. "Lichens in Relation to Forest Site Values." *The Bryologist*, **34**, pp. 66–71. 1931. (1. 201.)

In 1928 and 1929 the author was one of a small party consigned to do forest research work: to find out whether Cajander's "theory of forest types" was applicable to Canada. The ground covered was the western part of the province of Alberta, extending from near Crow's Nest Pass in the south to Lesser Slave Lake in the north. Most of the work was done in the more northern regions. Here the great forested areas are almost continuous; they are situated at a much lower altitude, and have generally a greater rainfall. The botanical ground covered included the flowering plants, mosses, hepatics, and lichens; in Brinkman's paper the lichens alone are dealt with.

The lichens studied are purely sylvicolous, none being gathered outside the range of the forests, and very few higher than 6 ft. from the ground. Even under these limiting circumstances the list is rather a considerable one. As the main purpose was to discover just which lichens had a bearing on the problem in hand, all were collected, but as the work progressed it became increasingly apparent that only a part of those collected had any bearing. For with lichens, as with flowering plants, some species are found to range through the whole gamut of forest types and so can have little significance for the present purpose. Thus *Peltigera* was found to range from the lowest to the highest forest type, but whether *P. aphthosa* and *P. canina* have a tendency to occupy different site values the author cannot say. There is undoubtedly a strong tendency for the broad deep-green forms to occupy the better sites, and the small somewhat shrunken greyish forms to abound on the poorer sites. Likewise the genus *Parmelia* does not seem, at present, to have much bearing on the subject, though a closer study of a few of the more commonly occurring species may yet show them to have some indicating value.

The list of species finally selected as having value was found to correspond pretty closely to that given by Ilvessalo of Finland. Those having most bearing on the subject were used in drawing up the two plot tables which accompany the paper and which are discussed by the author. It was finally concluded that the genus *Cladonia* (as represented by *C. rangiferina*, *C. alpestris*, and *C. sylvatica* with their nearest allies), *Cetraria islandica*, *Stereocaulon paschale*, and possibly *Icmadophila ericetorum* (when common enough) had significance. The group of Cladonias mentioned were found to be plants of the poorer forest site values; this was also true of the *Stereocaulon* and *Cetraria*; they were found to be occupants of sites of medium or low quality value. Cladonias occupying rotten logs were found on the medium to good sites. In the highest quality sites lichens were frequently absent, at least those spoken of above which were used as indicators.

At the end of the paper is given an alphabetical list of lichens of the western forested part of Alberta. This includes 54 species.

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

739. Barker, W. *"Lachenalia Mathewsii."* *Flowering Pl. S. Afr.* **11**, Pl. 422. 1931. (2. 135.)

This new species of Liliaceae was found growing on damp ground near Vredeberg, Malmesbury Division, South Africa.

740. Barker, W. *"Massonia Bolusiae."* *Flowering Pl. S. Afr.* **11**, Pl. 429. 1931. (2. 136.)

Massonia Bolusiae (Liliaceae) is a Karroo species from near Middelburg.

741. Verdoorn, I. C. *"Tulbaghia fragrans."* *Flowering Pl. S. Afr.* **11**, Pl. 438. 1931. (2. 137.)

Tulbaghia fragrans (Liliaceae) is a native of the Lydenburg district, Transvaal.

742. Verdoorn, I. C. *"Caralluma ubomboensis."* *Flowering Pl. S. Afr.* **12**, Pl. 443. 1932. (2. 138.)

This new member of the Asclepiadaceae was collected in the Ubombo Mountains, Natal.

743. Phillips, E. P. *"Stapeliopsis Cooperi."* *Flowering Pl. S. Afr.* **12**, Pl. 445. 1932. (2. 139.)

The new genus *Stapeliopsis* (Asclepiadaceae) has affinities with both *Stapelia* and *Caralluma*. The only species described is based on *Stapelia Cooperi* N.E.Br.

744. Verdoorn, I. C. *"Huernia bicampanulata."* *Flowering Pl. S. Afr.* **12**, Pl. 449. 1932. (2. 140.)

Huernia bicampanulata (Asclepiadaceae) grows among loose boulders and between stones under thorn trees. It is found in the Pietersburg district, Transvaal.

745. Phillips, E. P. *"Huernia Vogtsii."* *Flowering Pl. S. Afr.* **12**, Pl. 452. 1932. (2. 141.)

This species is from the Rustenburg district, Transvaal.

746. Phillips, E. P. *"Huernia confusa."* *Flowering Pl. S. Afr.* **12**, Pl. 456. 1932. (2. 142.)

H. confusa grows along the edge of rocky outcrops near Haenertsburg, Pietersburg district, Transvaal.

747. Phillips, E. P. *"Euphorbia maleolens."* *Flowering Pl. S. Afr.* **12**, Pl. 459. 1932. (2. 143.)

748. Phillips, E. P. and **Letty, C.** *"Stapelia forcipis."* *Flowering Pl. S. Afr.* **12**, Pl. 460. 1932. (2. 144.)

This new species of Asclepiadaceae is a native of the Port Elizabeth district of the Cape Province.

749. Rendle, A. B. "African Notes. II." *Journ. of Bot.* **70**, pp. 73–78. 1932. (2. 145.)

A list is given of the more interesting species collected during a visit to Africa. Several new species are described including one, *Senecio* (*Kleinoidei*) *carnosulifolius* S. Moore, from the Knysna district, South Africa.

750. Baker, E. G. "New African Species of Leguminosae." *Journ. of Bot.* **70**, pp. 251–255. 1932. (2. 146.)

Lotononis (*Krebsia*) *Brierleyae* from the Orange Free State is the only species described from South Africa.

751. "Novitates Africanae." *Journ. of Bot.* **70**, pp. 282–287. 1932. (2. 147.)

A new species of *Oxalis* is described by T. M. Salter and new species in the genera *Crassula*, *Agathosma* (Rutaceae), *Acmadenia* (Rutaceae), and *Dicoma* (Compositae) are described by R. H. Compton.

752. Brown, N. E., Tischer, A. and Karsten, M. C. *Mesembryanthema.* Pp. i–xxvi + 1–323, Frontisp., Plates 1 and 2, Figs. 1–167. 1931. (2. 148.)

The book includes a chapter on the ecology of the Mesembryanthema contributed by Miss M. C. Karsten in which free use has been made of previous publications of R. Marloth and K. Dinter on the same subject. A chapter by Dr Tischer is devoted to the cultivation, while Dr N. E. Brown is responsible for the description of the species each of which is accompanied by a photograph. Most of the illustrations are of cultivated plants but there are several showing the habitats of the species.

753. Davy, J. Burtt. *A Manual of the Flowering Plants and Ferns of the Transvaal with Swaziland, South Africa.* Part II. Malvaceae to Umbelliferae. Pp. i–xxxvi + 273–529, Figs. 41–80. 1932. (2. 149.)

In this further part the author has had the assistance of specialists in the elaboration of certain genera. Preceding the enumeration of the families there are published diagnoses of the new species and varieties and also a number of new combinations.

754. Bolus, L. "Plants New and Noteworthy." *S. Afr. Gard. and Country Life*, **22**, pp. 57, 59, 83–84, 88, 109–110, 137, 143, 229, 232, 243, 253, 275–276, 277, 6 Figs. and 6 Photos. 1932. (2. 150.)

In this series new species are described in the following genera: *Ammocharis* (Amaryllidaceae), *Babiana* (Iridaceae), *Brunsvigia* (Amaryllidaceae), *Cryptostephanus?* (Amaryllidaceae), *Ferraria* (Iridaceae), *Geissorhiza* (Iridaceae), *Gethylis* (Amaryllidaceae), *Kaempferia* (Zingiberaceae), *Lithops* (Aizoaceae), *Moraea* (Iridaceae), *Nerine* (Amaryllidaceae), *Ornithogalum* (Liliaceae), *Pachypodium* (Apocynaceae), *Pelargonium* (Geraniaceae), *Sarcocaulon* (Geraniaceae), and *Sparaxis* (Iridaceae).

755. Hutchinson, J. "*Erythrophysa alata.*" *Bull. Misc. Inf., Kew*, pp. 149–151, 1 Fig. 1932. (2. 151.)

Fagara alata Eckl. and Zeyh. is shown to antedate *Erythrophysa undulata* E. Mey. (Sapindaceae) which becomes *E. alata* (Eckl. and Zeyh.) Hutch.

756. Stent, Sydney M. "Notes on African Grasses. XII." *Bull. Misc. Inf., Kew*, pp. 151–152. 1932. (2. 152.)

Anthephora aequiglumis Goossens from the Orange Free State is referred to a new genus *Tarigidia* which is regarded as related to *Digitaria* Hall.

757. Dyer, R. A. "Notes on the Flora of Southern Africa." *Bull. Misc. Inf., Kew*, pp. 152–155. 1932. (2. 153.)

The following points are noted: *Pavonia Burchellii* (DC.) Dyer (based on *Althaea Burchellii* DC. and including *Pavonia Kraussiana* Hochst.); *Pavonia Meyeri* Mast (*P. columella* Auct.) is distinct from the true *P. columella* of Bourbon; *Corchorus arenicola* Hochr. is reduced to *C. aspleniifolius* Harv.; *Hermannia stellulata* (Harv.) K. Schum. said to be from Bechuanaland not Grahamstown; *H. jacobeifolia* (Turcz.) Dyer a new name for *H. bipinnata* (Linn.) Glover non Burchell; *H. resedifolia* Dyer is separated from *H. jacobeifolia*; some South African Statices are referred to *Limonium* Mill.

758. Phillips, E. P. "*Inezia*, a new genus of Compositae from South Africa." *Bull. Misc. Inf., Kew*, pp. 297–298. 1932. (2. 154.)

Inezia is based on *Lidbeckia integrifolia* Klatt; it is allied to *Lidbeckia*.

759. Bolus, L. "New South African Iridaceae." *Bull. Misc. Inf., Kew*, pp. 326–330. 1932. (2. 155.)

Homeria odorata, Hexaglottis nana, Watsonia Ryderae, W. Emiliae, W. pauciflora, W. Hutchinsonii, W. Leipoldtii, W. Archbelliae and *W. Comptonii* are described as new.

760. Summerhayes, V. S. "African Orchids." *Bull. Misc. Inf., Kew*, pp. 338–344. 1932. (2. 156.)

Habenaria Dinteriana Kraenzl. is reduced to *H. armatissima* Rchb. f.

761. Schuurman, J. F. M. "A Seasonal Study of the Microflora and Microfauna of Florida Lake, Johannesburg, Transvaal." *Trans. Roy. Soc. S. Afr.* **20**, pp. 333–386. 1932. (2. 157.)

The plankton of this shallow artificial lake was studied and a marked seasonal variation found. A list of 50 species identified by Miss F. Rich is published.

762. Young, Elaine M. "The Parasitism of *Harveya speciosa* Bernh." *Trans. Roy. Soc. S. Afr.* **20**, pp. 387–397, Figs. 1–10. 1932. (2. 158.)

The authoress reduces C. A. Smith's *H. anisodonta* on the grounds that the ovary is always glabrous and was wrongly described by Hiern. She notes that this species has several hosts, *Berkheya radula* (Harv.) Burtt Davy, *Conyza podocephala* DC., *Haplocarpha scaposa* and a grass.

763. Lavis, M. "A new *Conophytum* from Namaqualand." *S. Afr. Gard. and Country Life*, p. 257, 1 Photo. 1932. (2. 159.)

Conophytum approximatum (Aizoaceae) is described from specimens collected near Springbok, Little Namaqualand.

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

764. Lucas, A. H. S. "The Caulerpas of Victoria." *Victorian Naturalist*, Melbourne, **48**, pp. 84–93, 6 Text-figs. September 8th, 1931. (3. 53.)

Sixteen species of the genus are recorded from Victoria. Short descriptions of all are given, while a key is provided to the five species of Section Hippuroideae. Notes on distribution and habitat are added for most species.

765. Osborn, T. G. B., Wood, J. G. and **Paltridge, T. B.** "On the Autecology of *Stipa nitida*, a study of a Fodder Grass in Arid Australia." *Proc. Linn. Soc. New South Wales*, Sydney, **56**, pp. 299–324, Plate 18, 14 Text-figs. October 15th, 1931. (3. 54.)

The investigations described in this paper were carried out at the Koonamore Vegetation Reserve in the north-eastern district of South Australia.

Stipa nitida is the most important fodder grass in the north-east of South Australia. Plants only reach full maturity, forming large tussocks, on sandy or sand-loam soils. On such soils the species may form a constituent of any of the major communities in arid South Australia. The root system consists of a fairly compact surface-rooting portion and a more diffuse deeper-rooting part extending to a depth of over 40 cm. By means of this double root system the plant is able to utilise light falls of rain that wet the surface soil only, in addition to tapping the deeper water reserves of the soil. The ideal seed-bed is of sand. Litter, consisting of the dead remains of other herbage, plays an important part in entangling the fruits of the grass. Seedlings fail to reach maturity on hard loamy soil. The percentage germination of the seed is low. Laboratory experiments have shown that the soil must be saturated and that light is a factor. Observations show that germination in the field is best following late summer rains.

The influence of grazing has been studied by means of quadrats both inside the Reserve and also in the adjacent paddocks. By utilising "index numbers" which express the ratio between the plants growing inside or outside the Reserve and the total number of plants, it has been shown that the balance between the plants inside and outside the fences has been seriously affected by the combined effects of grazing and drought during the period of the investigation. It is shown that the intense drought conditions are not the only adverse factors affecting the grass outside the Reserve. Sheep have a profound effect by killing potential seed plants through trampling and grazing, and the bare soil thus formed becomes very unstable. Heavy rain or wind removes this and leaves a hard loamy soil unfavourable for germination of the grass. Careful control of grazing during drought periods is necessary to maintain an adequate population of *Stipa nitida*.

766. Thomas, L. A. "The Re-advancement of the Vegetation over the Mined Areas of Bendigo." *Proc. Roy. Soc. Victoria*, Melbourne, **44**, pp. 77–91, Plates 9 and 10, 3 Text-figs. February 29th, 1932. (3. 55.)

The area dealt with is about 700–800 ft. above sea-level. The mean annual rainfall is about 21 in., and falls mostly during the winter. Droughts occur occasionally. The normal soil is derived from Ordovician strata, and consists of stiff clay or hungry sands. There is also alluvium in the river valleys. The deposits following mining consist of heaps of unweathered quartz, etc., and finer material obtained after crushing for gold extraction. Both these deposits are unfavourable for plants. The natural vegetation of the area is an open *Eucalyptus* forest dominated by *E. sideroxylon*, *E. polyanthemos* and *E. macrorrhyncha*.

A list of the species forming the community is given. Each dominant also occurs in places as a pure consociation. *E. viridis*, a plant characteristic of areas with lower rainfall, occurs in certain belts. The main stratum societies are formed by *Cassinia arcuata*, a shrub about 3–8 ft. high, and species of *Juncus*.

As a result of mining operations the original vegetation has been destroyed in most places. Mining was suspended sixteen years ago and now the bare areas are being re-invaded by the plants around. An intensive study of this invasion was made in a valley about three miles long. The chief invader of the mined areas is *Cassinia arcuata*, other important species being *Acacia pycnantha*, *Vittadinia australis* and *Melaleuca decussata*. The conditions governing the spread of the *Acacia* are discussed. Another abundant species is *Juncus pallidus*, which forms extensive societies on almost all kinds of soils. Other species of *Juncus* also occur, but usually only in damper places. There seems to be no long succession of seral communities. The dominant shrubs and herbs of the *Eucalyptus* forest are merely re-establishing themselves in the absence of the trees, which show little sign of invading the areas.

767. Cunningham, G. H. "The Gasteromycetes of Australasia. XIV. The Family Tulostomataceae." *Proc. Linn. Soc. New South Wales.* Sydney, **57**, pp. 27–39, Plate 1, 7 Text-figs. May 16th, 1932. (3. 56.)

This family includes five genera and nineteen species in Australasia. A key to the genera is provided, and also descriptions of all the species except those of the genus *Tulostoma*, which has been dealt with in a previous paper. An artificial key to the species of this genus is given instead.

<center>(4) NEW ZEALAND (COLLABORATOR, V. S. SUMMERHAYES)</center>

768. McIndoe, K. G. "An Ecological Study of the Vegetation of the Cromwell District, with Special Reference to Root Habit." *Trans. New Zealand Institute*, Wellington, **62**, pp. 230–266, Plates 38–41, 3 Maps, 17 Text-figs. March 31st, 1932. (4. 40.)

The area studied lies in the upper Clutha Valley of Central Otago. The mean annual rainfall is about 15 in. distributed evenly throughout the year, but owing to differences in evaporation the soil is wet during the winter and dry during the summer. The temperatures are very high during the summer, while during the winter the ground is often frost-bound for considerable periods. Violent dry north-westerly winds are not infrequent in the summer. On either side of the valley are mountain ranges from 5000–6000 ft. in height. The soil is of varying depth and nature, but is on the whole very fertile. Much of it is extremely porous and rain is rapidly absorbed.

Most of the communities below 3000 ft. owe their nature to the influence of fire, sheep and rabbits. The original tussock grassland in many places has been replaced by the xerophytic *Raoulia lutescens*. Above 3000 ft. the greater rainfall has enabled the grassland to survive. The area can be divided into four main regions according to the vegetation.

(1) The lower slopes of the Dunstan Range. Here *Raoulia lutescens* is dominant. In the spring a number of small annuals appear between the *Raoulia* cushions. A few small shrubs occur scattered over the slopes.

(2) The lower slopes of the Pisa Range. These face south, and here the tussock grasses *Poa caespitosa* and *P. Colensoi* are dominant. *Raoulia* occurs only on dry ridges.

(3) The river bottom terraces. On the absorbent gravels of this area only scattered *Raoulia* plants, certain small annuals and a few mosses and lichens are found. *Poa caespitosa* is absent.

(4) The Cromwell sandy flat. *Poa caespitosa* is usually dominant on the drifting sand covering this area, but *Raoulia* predominates where the sand layer is lacking or is less than 6–9 in. deep.

The root systems of a number of the most important species were examined by means of the trench method. The leaf anatomy of some of these was also investigated. The relationships of these root systems to the soil conditions is discussed. In three species both superficial and deep absorbing root systems were produced.

769. Cockayne, L., Simpson, G. and **Scott Thomson, J.** "Some New Zealand indigenous-induced Weeds and indigenous-induced modified and mixed Plant Communities." *Journ. Linn. Soc.* London, Botany, **49**, pp. 13–44, Plates 3–7. June 23rd, 1932. (4. 41.)

The authors show that the belief that indigenous plants are unable to compete successfully with introduced plants in any habitats in New Zealand is an error. On the whole the introduced species are restricted to areas where the natural conditions have been profoundly disturbed by man or his grazing animals, whereas the indigenous species predominate on undisturbed areas. The exotics also become less important as the altitude increases. In some cases in disturbed areas indigenous species have become troublesome weeds, while in others quite new communities composed of indigenous species have been formed. These are termed "indigenous-induced" weeds and communities respectively. The conditions leading to the appearance of such are discussed and many examples are given. In certain areas indigenous-induced communities have replaced those formed of exotic species, while the invasion of communities of introduced plants by indigenous species is taking place in many other localities.

770. Cockayne, L. and **Sledge, W. A.** "A Study of the Changes following the Removal of Subalpine Forest in the Vicinity of Arthur's Pass, Southern Alps, New Zealand." *Trans. Linn. Soc.* London, Botany, **49**, pp. 115–131, Plates 20 and 21. September 30th, 1932. (4. 42.)

The area dealt with lies at 850 ft. altitude in the upper Bealey Valley. Twenty-four years ago the subalpine *Nothofagus cliffortioides* forest was burnt and new communities have since been developed. A description of the original forest is given, followed by that of the new communities. The chief vegetation consists of a mixture of herbaceous plants and dwarf shrubs with isolated shrubs or groups of shrubs scattered about. This "Shrub herb-field" can be divided into shrub-land, herb-field and bogs. The chief shrubs are *Dracophyllum longifolium* and *Cassinia Vauvilliersii*. *Nothofagus cliffortioides* is rare and shows no indication of future re-dominance. A list of all the vascular plants in the new areas is provided together with their habitats and frequencies. The chief mosses and lichens are also listed.

(7) INDIA, BURMA AND CEYLON (Collaborator, R. J. D. Graham)

771. Parker, R. N. "A Burmese climbing Bamboo. *Klemachloa* R. N. Parker gen.nov." *Indian Forester*, Allahabad, **58**, pp. 7–9, Plate 1. January, 1932. (7. 158.)

Klemachloa detinens, a new species of a new genus of Bamboo belonging to the Eubambusae is described.

772. De, R. N. "A trip down the Simsang valley of the Garo Hills." *Indian Forester*, Allahabad, **58**, pp. 36–39, Plates 2 and 3. January, 1932. (7. 159.)

A brief description of an area in Assam in which Sal is the main crop on the hill tops, *Odina wodier* and *Schima Wallichii* occurring where the Sal is unprotected, but evergreen forest with *Mesua ferrea*, *Isonandra polyantha*, *Cynometra polyandra* occurs in the valleys. *Nepenthes* is recorded from this area.

773. Singh Sher. "A note on the regeneration of Deodar in the Udil Range, Ramban Division, Tammer, with special reference to the eradication of Pohu (*Parrotia jacquemontiana*)." *Indian Forester*, Allahabad, **58**, pp. 75–81. February, 1932. (7. 160.)

The advantages of the Shelterwood system over the selection system in the deodar forests of Kashmir are emphasised. The success of the first system is stated to depend on the eradication of Pohu. The method recommended is killing of standing trees by burning debris at their base. Retention of Pohu is however advocated by Jamwall (**781**).

774. De, R. N. "Taungya in the Garo Hills, Assam." *Indian Forester*, Allahabad, **58**, pp. 93–99, Plates 5 and 6. February, 1932. (7. 161.)

A detailed account of working a system for regeneration of Sal associated with the cultivation of cereal crops.

775. Champion, H. G. "The mode of growth of *Alstonia scholaris* R.Br." *Indian Forester*, Allahabad, **58**, pp. 123–124, Plate 7. March, 1932. (7. 162.)

An illustrated account of the peculiar sympodial growth in the stem of this tree.

776. Raizada Mukat Behari. "New Indian Species of Forest Importance." *Indian Forester*, Allahabad, **58**, pp. 133–140. March, 1932. (7. 163.)

133 species are listed.

777. Smythies, E. A. "Sal and its regeneration in the United Provinces." *Indian Forester*, Allahabad, **58**, pp. 196–120. April, 1932. (7. 164.)

An historical summary of the conflicting views on methods for Sal regeneration is given and the suggestion that Sal must usually be regarded as a stage in the progression of an area is used to reconcile discordant recommendations.

778. Garland, E. A. "Succession among the grasses of the Deccan trap dry mixed deciduous formation and its use in sub-classification." *Indian Forester*, Allahabad, **58**, pp. 221–224. April, 1932. (7. 165.)

Colonisation of Deccan trap with rainfall between 60 and 20 inches can be subdivided into six stages. (1) Much bare rock and earth thinly covered with *Aristida* spp. and some *Andropogon contortus*. *Andropogon monticola* on deeper soil deposits. Few xerophytic shrubs. (2) *Andropogon contortus* increases largely associated with *A. monticola*. *Aristida* spp. still present. Shrubs and dwarf trees under 6 ft. "Lantana" apt to become invasive. *Apluda varia* appears under shrubs. (3) *Andropogon contortus* co-dominant with *A. monticola* and *A. pertusus*, *Apluda varia* sub-dominant. Tree species average 12 ft., *Boswellia serrata*

is the only or principal representative. Shrubs may or may not have spread. (4) *Andropogon contortus* definitely dominant and *A. monticola* and *A. pertusus* co-dominant with *Ischaemum laxum* or *I. sulcatum*. Tree species, teak on reddish soils and *Anogeissus latifolia* on grey friable soil, average 20 ft. Tree canopy forming in favourable sites. (5) *Anthistiria ciliata* appears and *Andropogon contortus* disappears. Tree species average 30 ft. and suppress shrubs. Marked increase in natural regeneration of tree species, especially *Terminalia tomentosa*. (6) Closed tree canopy of mixed deciduous trees averaging 30–50 ft. Shrubs have disappeared. *Anthistiria ciliata* strongly dominant in open glades.

779. Singh Bahadur. "Irrigated plantations in the Punjab." *Indian Forester*, Allahabad, **58**, pp. 247–251, Plates 10 and 10 a. May, 1932. (7. 166.)

A general account of the establishment of plantations of *Dalbergia Sissoo* to replace arid scrub forests containing *Prosopis spicigera*, *Capparis aphylla* and *Tamarix articulata*.

780. R. M. G. "'Paget M.P.' looks at Sal." *Indian Forester*, Allahabad, **58**, pp. 255–261, Plates 11 and 12. May, 1932. (7. 167.)

Reference is made to Sal regeneration by natural ecological development as advocated by Davis (**669**) and Chahirvedi (**670**) and to that by "Taungya" described by Bhola and Hussain (**695**). Recommendations for limiting damage by deer and for the use of cover crops, amongst others *Tephrosia candida*, are given.

781. Jamwall, H. S. "The eradication of *Parrotia jacquemontiana* from the Conifer Forests of Kashmir." *Indian Forester*, Allahabad, **58**, pp. 317–322. June, 1932. (7. 168.)

Arguments are put forward on sylvicultural and economic grounds for the retention of this, the only deciduous shrub in the Kashmir Conifer Forests. Eradication is recommended by Singh (**699**).

782. Dastur, R. H. and **Cooper, R. E.** "The osmotic and suction pressures of the rice plant, *Oryza sativa* L., when treated with salts. A method of determining the salt requirements of plants." *Ind. Journ. Agri. Sci.* Calcutta, **2**, Part 2, pp. 99–137. April, 1932. (7. 169.)

Changes in osmotic and suction pressures of roots and leaves of rice in cultures with ammonium sulphate and potassium nitrate are recorded as higher in the case of ammonium sulphate. Chemical analysis showed absorption of the ammonium and sulphate ions whereas only traces of the nitrate ion were absorbed. Confirmatory tests were obtained in pot cultures in soil and pure sand.

Single salt cultures in calcium sulphate and potassium sulphate showed higher values with calcium, the calcium being absorbed. Cultures of rice, *Tradescantia zebrina* and *Zea mays*, showed a rise in the presence of required salts and a depression in its absence. It is suggested that the most essential of the salts required by plants can be determined by changes in the osmotic and suction pressures of their roots and leaves.

783. Blatter, E. and **Millard, W. S.** "Some beautiful Indian Trees." *Journ. Bombay Nat. Hist. Soc.* **35**, pp. 525–529, Col. plates 15 and 16, Plates 16 and 17, Text-fig. 6. February, 1932. Pp. 824–825, Col. plate 17, Plate 18, Text-fig. 2. July, 1932. (7. 170.)

Sterculia colorata, *Lagerstroemia flos-reginae* and *Cordia sebestena* are illustrated and described.

(8) TROPICAL AND NORTH AFRICA (COLLABORATOR, E. MILNE-REDHEAD)

784. Chipp, T. F. "The Vegetation of Northern Tropical Africa." *Scottish Geographical Magazine*, **47**, pp. 193–214, 4 Plates, 4 Maps, 1 Figure. July, 1931. (8. 84.)

The West African Botanical Region here being considered has two endemic floras, that of the Sudan, an open-country flora, and that of the West African and Congo forests. These great tropical forests may be looked upon as the greatest developments of the vegetation in Africa. Centering on the Cameroons they stretch out east, north and west, giving place to a more open type of vegetation as more arid conditions obtain.

The natural factors which operate over the West African Botanical Region are considered. Firstly the climate, the chief features of which are the steady north-east trade winds which are very dry, and the periodic monsoon from the Gulf of Guinea which is moisture laden. The heaviest rainfall is therefore around the Gulf of Guinea, and there is a gradual diminution of rain as one proceeds inland, until one reaches the Sahara desert where the desiccating north-east trade winds predominate. Further climatic information is given together with some diagrammatic climate charts. Secondly the most prominent edaphic factor is mentioned, namely the amount of soil moisture. Thirdly the physiographic factor is shown in the local climates created by the great mountain masses, such as the Cameroons Mountain.

The chief climatic types of vegetation are then considered. (1) The Closed Forest, which was at one time more extensive than it is now, covers a large part of the Congo basin, and then stretches northwards at its optimum development through the Cameroons and into Southern Nigeria, and intermittently as far west as Sierra Leone. The Fringing Forests of the rivers are said to be one piece of evidence as to the former extent of the Closed Forest. (2) The Grass-woodland is the next type of vegetation, and it circles round the Closed Forests and is an expression of diminished precipitation. It is not so homogeneous in its composition as is the Closed Forest, and in the definite dry period it is swept by fires which tend to destroy its natural wealth. (3) The Thorn Scrub, still farther north, is the last great vegetational belt. Like the Grass-woodland, this belt extends right across Africa from the Atlantic to the Abyssinian Plateau. (4) The Ephemeral Grass-Herb vegetation is that of the desert region, and only springs into life after one of the rare showers. It is composed of herbs which are able to mature their fruit in a few days.

Edaphic types of vegetation are then mentioned, namely the Mangrove of the coast, the reed and Papyrus swamps inland, and the vegetation of the dry watercourses of the desert region. The montane vegetation of the Tropical African Mountains, so distinct from the climatic and edaphic vegetation of the Continent in general, appears as a distinct type superimposed on the vegetation of Africa itself. The influence of man on the vegetation of this region is mentioned, and some economic aspects of the vegetation are reviewed.

785. Baker, E. G. and **Exell, A. W.** "A new genus of Connaraceae from Tanganyika Territory." *Journ. Bot.* **69**, pp. 249–251, 1 full-page figure. October, 1931. (8. 85.)

Burttia prunoides Bak. fil. et Exell is described. It is a dominant shrub in the great thicket areas of the Singida and Kondoa Districts of Tanganyika Territory.

786. Varian, H. F. "The geography of the Benguella Railway." *Geographical Journ.* **78**, pp. 497–523, 4 Plates, 1 Map. December, 1931. (8. 86.)

A general account of the country through which the Benguella Railway passes is given, with only brief mention of the vegetation.

787. Stevenson, T. "The Flora of Algeria." *Journ. Bot.* **69**, pp. 305–309. December, 1931. (8. 87.)

The physical features of Algeria are briefly summarised as (1) the coastal plains, (2) the Northern Atlas ranges, attaining a height of 5000–6000 ft., (3) the high plateau between the Northern and Southern Atlas ranges, and (4) the Sahara Desert. The more striking and interesting plants met with by the writer, who was in Algeria in the months of April and May, are mentioned.

788. Bullock, A. A. "*Canthium* in British East Africa." *Kew Bull. Misc. Inform.* London, 1932, pp. 353–389, 4 full-page figures. 1932. (8. 88.)

The Rubiaceous genus *Canthium* Lam. (*Plectronia* L.) is tentatively arranged as far as its British East African species are concerned. Forty-five species are recognised, sixteen of which are new.

(9) CENTRAL AND SOUTH AMERICA (COLLABORATOR, R. C. McLEAN)

789. Hardy, F. and **Griffiths, G.** "Carbon/Nitrogen Ratios in Cacao Soils." *Nature*, **129**, 1932, p. 132. January 23rd, 1932. (9. 20.)

Profile samples collected in Tobago in 1930 showed a close correlation between yielding capacity and the carbon/nitrogen ratio for the organic matter in the first 6 in. of soil. The mean ratio for "good" soils is 8·3 and for "bad" soils is 6·8. Statistically this correlation has a much higher significance than the correlation with the total organic matter present. Ratios of the same order of magnitude, though not identical, were found in Cacao soils from Trinidad and Grenada. Climatically these three areas are similar, but the soil types are markedly different. Further studies are in progress.

790. Gill, Tom. "Tropical Forests of the Caribbean." *Tropical Plant Research Foundation*, in co-operation with the Charles Lathrop Pack Forestry Trust. Pp. 318 and xix, Plates 81. 1931. (9. 21.)

An account of the results of exploration organised by the above Trust and extending over three consecutive winters, with the objects of original collecting and of correlating previous information. The ground covered included Trinidad, British Guiana and British Honduras, besides other Tropical American lands outside the Empire. Aeroplane, horse and canoe were all used as transport. The questions indicated for consideration were: how much timber is there, what sorts does it consist of and what is it good for?

The first five chapters are devoted to a general survey of tropical timber resources and tropical forestry, in the light of the world's needs of timber. Chapter VI deals with British Forestry Policy in Tropical America, and here the British are credited with the most thorough and successful attempts at Forestry in that region of the world. The need of a scientific Forest Policy for Jamaica is specially urged. The remaining chapters deal with non-British countries in Tropical America and with suggestions for future development, technical and financial.

An appendix gives the better-known species of broad-leaved trees in the Caribbean, taxonomically arranged. There is also a Bibliography and a Glossary of Common Names.

SOIL ACIDITY IN RELATION TO VEGETATIONAL SUCCESSION IN CALTHORPE BROAD, NORFOLK

By H. GODWIN and J. S. TURNER.

(With ten Figures in the Text and one Folding Transect.)

CONTENTS.

INTRODUCTION.

THE river valleys of the Bure, Yare, Thurne and Waveney contain extensive fenlands and the large system of shallow lakes known as the Norfolk Broads. These have always commanded the attention of naturalists, but extremely little systematic study of their plant ecology has been made. The competent pioneer work of Miss M. Pallis (4), in *Types of British Vegetation*, remains our only substantial account of them from the vegetational point of view.

The open water of the Broads is alkaline in reaction (presumably due to drainage from chalk-bearing glacial drift) and the vegetation is generally regarded as typical of "Niedermoor." At the same time acidiphilous species have long been known to occur in the Broads area, but so many outcrops of sand and gravel occur among the peat that these have not received much attention and even where such species have been demonstrated to be growing on peat, no special importance has been attached to them and they have been referred to merely as extensions of acidic upland plant communities, or as sporadic communities.

Miss Pallis's comments on Sphagneta and Calluneta growing on peat near Potter Heigham show this viewpoint. "The position of this and other moor associations close to the upland, suggests that they may be regarded as the wet continuations of heaths which probably occupied the upland soil before the days of cultivation."

"The Sphagneta are rather to be regarded as a sporadic development of moor in certain favourable spots."

Miss Pallis carried out her valuable pioneer work before soil acidity had been extensively investigated either as regards its origin or as regards its effects in controlling vegetational distribution, and she therefore makes no suggestion of the possibility of a natural development of Sphagneta and moors from Broadland aquatic vegetation. The writers of this paper take just this point of view and attempt to establish that in some cases, at least, the presence of acidiphilous species is an indication of the progression of vegetational development normal for the region, which will tend eventually to produce acid peat, even though the Broads are themselves definitely alkaline to begin with. In support of this, an account is given of the vegetational successions and the occurrence of acidiphilous species with measurements of soil acidity at Calthorpe Broad, near Hickling, Norfolk. The attention of the writers was first drawn to this on account of two facts. Firstly, it showed, as few Norfolk Broads do, well developed semi-natural oakwoods in apparent continuity with the typical fenland communities of reed-swamp, fen, and carr, surrounding the Broad concentrically. In the second place, in various parts of the property, where at a distance from the Broad the peat was fairly high above the water-table, occasional planted rhododendron bushes were flourishing. This striking development of a markedly acidiphilous genus was emphasised at once by the recognition in the carr undergrowth and in other places of extensive areas covered with tussocks of two or three species of *Sphagnum*. At a later stage, other acidiphilous species were also discovered. Preliminary determinations made at once in the field (using the colorimetric waxed paper method described by S. Cole) gave strikingly acid values for the peat soils round the Broad.

This suggested that it would be profitable to investigate the Broad from the point of view of determining what relation exists between the development of soil acidity and the progress of vegetational succession from the open and alkaline waters of the Broad towards woodland. In so far as the Broads region had traditionally been considered thoroughly representative of "Niedermoor" vegetation, the possibility that there might here be evidence of natural development to acidic types of soil and even to "Hochmoor" vegetation, the problem seemed one of the greatest general interest.

I. Locality and topography.

Calthorpe Broad (Fig. 1) lies on the extreme northerly border of the Norfolk Broads region, about 2 miles north of the largest of the Broads, Hickling Broad, and 3 miles north-west of Horsey Mere. It is not in navigable communication with the other Broads, and as it is also private and small, it is comparatively unknown. It has shrunk considerably in area during the last 50 years and now consists of a sheet of water about 250 m. long and 50 m. wide, surrounded by

reed-swamp, bushes and trees. It is connected by dykes with the drainage system of the country round about and in this way is in ultimate connection with Horsey Mere. Artificial water-level control by sluices and pumping mills appears to have been practised in the past, but the dyke system must have been quite different from the present one, and so far as is known no record
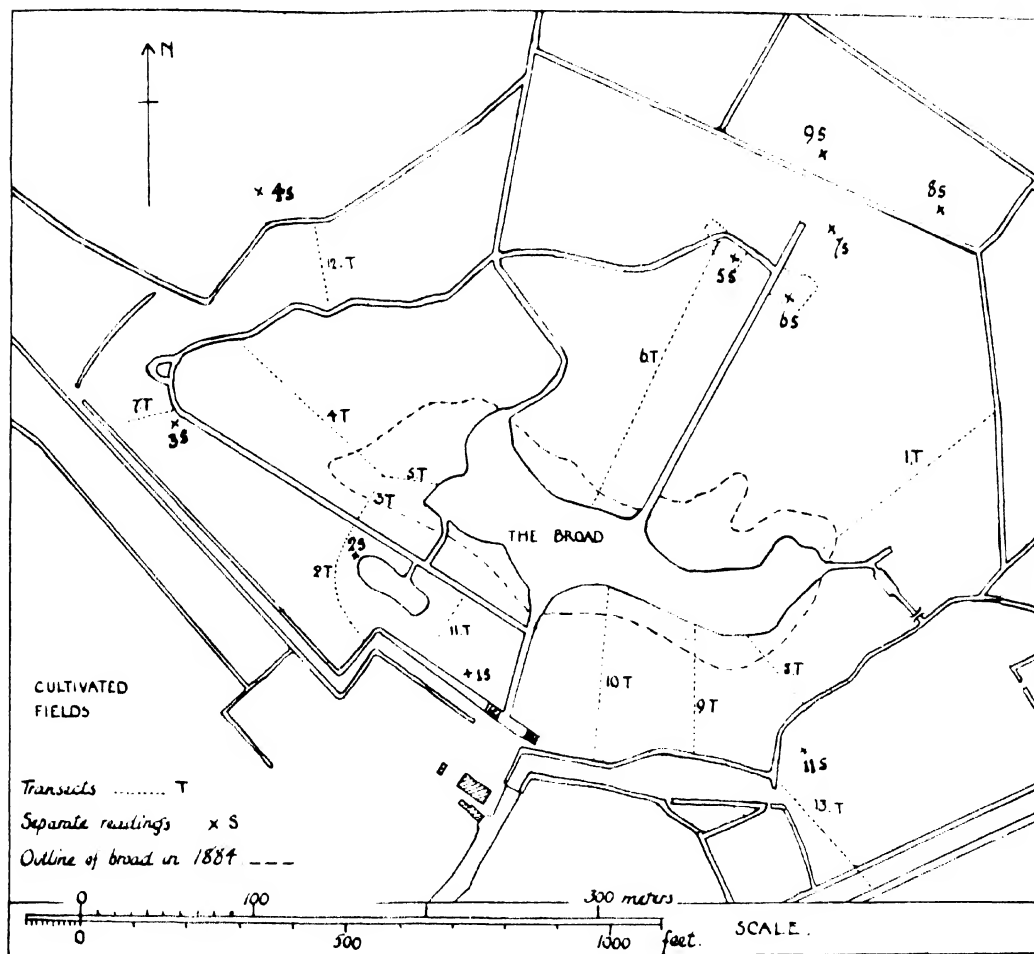
Fig. 1. Map of the area surrounding Calthorpe Broad, partly copied from 25 inch O.S. and partly surveyed by compass. It shows the position of all the open dykes and of the transects and separate sites in which observations were taken. Site 10 S is off the map, lying about 450 m. to the north-east of the extreme eastern end of the Broad, but within the Calthorpe basin.

exists of such past conditions. At the present time drainage from the surrounding country maintains the level of the water in the Broad, though in winter excess is pumped off into Horsey Mere. This control of the drainage system is one of the factors complicating the interpretation of successional phenomena in the region of the Broad and indeed of the Norfolk Broads in general.
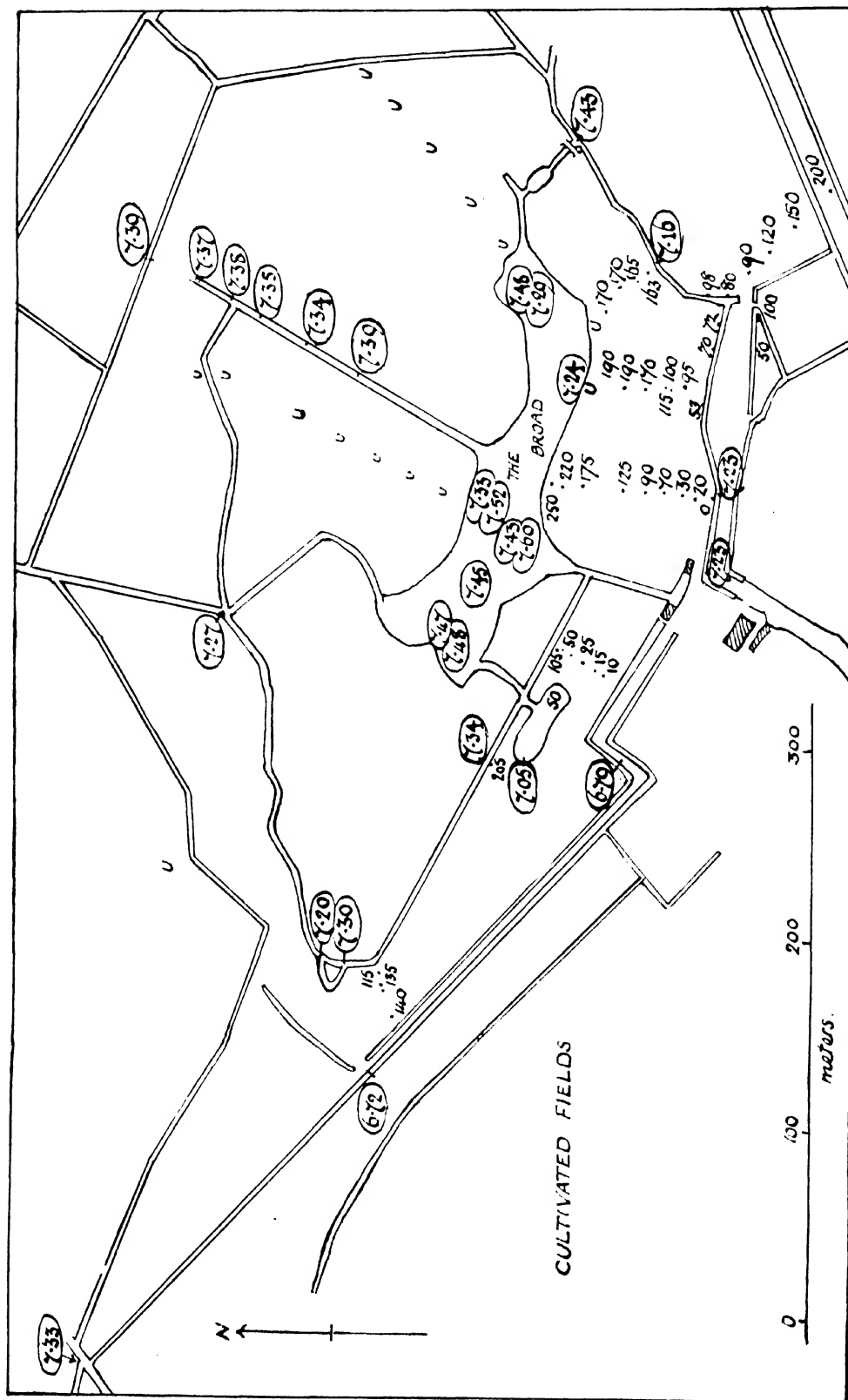
Fig. 2. Dual purpose map of Calthorpe Broad showing (a) by the smaller figures, the depth of hard silt below the soil surface in cm. (U = unknown depth greater than 2 m.); (b) by the large ringed figures, the results of electrometric pH determinations of the water of the Broad and of various parts of the dyke system.

The water of the Broad is alkaline in reaction like the rest of the Norfolk Broads, although its comparative isolation and distance from the sea (*via* open water channels) prevent the ingress of salt water which takes place in some others. The reaction of the water of the Broad has been measured several times and the pH value varies between 7·3 and 7·7. A number of measurements have also been made of the acidity at different points in the system of dykes connected with the Broad, and the results are shown in Fig. 2. The dykes traverse an area the surface soil of which is, as we shall see later, almost uniformly acid, and this fact explains the tendency towards neutrality at points in the dykes some distance from the Broad. The outer dyke along the south-east margin of the area is acidic, and this is almost certainly due to the fact that it can very seldom receive water from the Broad.

The total solutes in the water of the Broad (January, 1932) amount to 0·56 gm. per litre. The buffering capacity of the water was found by constructing the titration curve. From this it was possible to find figures for comparison with data for other natural waters of which the carbonate hardness has been determined by acid titration using methyl red (colour change at pH 5·2) or methyl orange (colour change at pH 3·75) as indicators. These figures are 140 and 175 parts per million respectively, the first of which may be compared with Pearsall's figures (7) for the soft waters of the Westmorland lakes which range from 0·5 to 16 parts per million, and the second with the figures obtained by the Laboratory Staff of the West Riding Rivers Board for the "slightly hard" waters of the River Wharfe (14). These range from 65 to 168 parts per million. The concentrations of carbonates in the "hard" waters of Wicken Fen, if calculated as entirely calcium carbonate, lie, according to Saunders (9), between 130 and 230 parts per million.

The Broad lies close to the southern side of a wide depression, and on this side the upland cultivated fields come within about 100 m. of the open water, while silty sand occurs at relatively small depths under the peat on this side of the Broad, the upper layers leached quite white by the acidic peat overlying them. By thrusting a long pole down through the thin surface peat and the soft swamp peat below, it was possible to tell with considerable accuracy the depth of the silt. Tests were made in this way all round the Broad and the results have been shown in Fig. 2. It will be seen that although the peat on the southern side of the Broad thins out against the sloping bank of the silt, that on the north side is considerably deeper, just how deep we are unable to say. What we refer to as "swamp peat" is a very soft wet yellowish brown peat containing remains of *Phragmites* and resembling closely the peat at present forming in the reed-swamp. This swamp peat extends over the whole Calthorpe area and suggests that it is by encroachment of reed-swamp that almost the whole basin has been converted from open water.

II. Vegetational succession and plant communities.

(1) *Vegetational succession.*

It is not now proposed to discuss the vegetational successions of Calthorpe in detail; indeed it would be difficult to do this without very extensive comparison with other Broadland areas, and without concentrated investigation of human influence both on vegetation by cutting, planting, clearing and on drainage by dyking and clearance of vegetation, draining and so forth.

Fortunately, however, the essential nature of the plant succession is simple. It may be written

<p style="text-align:center">open water → reed-swamp → carr → oakwood,</p>

although it may or may not be necessary to interpose a phase of "fen" between reed-swamp and carr, and although it is hardly certain that carr does in fact always give place to oakwood. Fig. 3 gives a conspectus of these major communities round Calthorpe Broad. The boundary between woodland and carr is that of the Ordnance Survey of 1905: it is not now very different. The map does not show the present distribution of carr but it gives the limit of its inward extension in 1884 and 1905; this is the lake margin and carr could hardly have occurred in the open water of the lake. The present outline of open water is sharp and artificial—it is due to cutting, especially just about 1919, for reed-swamp invaded the Broad extensively during the war period. The area just outside this line is partly reed-swamp and partly young carr, the latter occurring at different distances from open water in different parts of the Broad (see transects, Figs. 4–11).

(This map is not intended as an accurate guide to the present vegetational communities, nor has such a map been made, since the possible gain appeared quite disproportionately small in comparison with the labour involved. Repeated checks on the ground also show that the alterations from the given map would be in detail rather than in principle.)

The markedly concentric arrangement of the three major plant communities of reed-swamp, carr and wood is extremely striking, suggesting at once the validity of supposing them to represent successive stages of vegetational change accompanying progressive shallowing and retreat of the Broad. This conclusion is strongly supported by the evidence of the O.S. maps of 1884 and 1905 which repeatedly show areas in which carr has replaced reed-swamp or woodland has replaced carr. Nor would such a conclusion be difficult to support on general grounds, nor on the evidence of previous work in Norfolk. The most uncertain point in the hypothetical sequence is the transition from carr to woodland, for most of the large trees of zone *A* have certainly been planted, a large proportion of them being *Pinus sylvestris*, not now native in England. Nevertheless, the bulk of the trees, which are *Quercus robur*, have grown extremely well; not only are these pioneers 14–15 m. high,

with a very wide branch spread, but they have produced abundant trees of the F_2 type[1], also 13–16 m. high: regeneration appears to be taking place, and some possible invasion of the neighbouring carr. These facts suggest that in the presence of adequate seed parents, *Q. robur* wood might quite con-
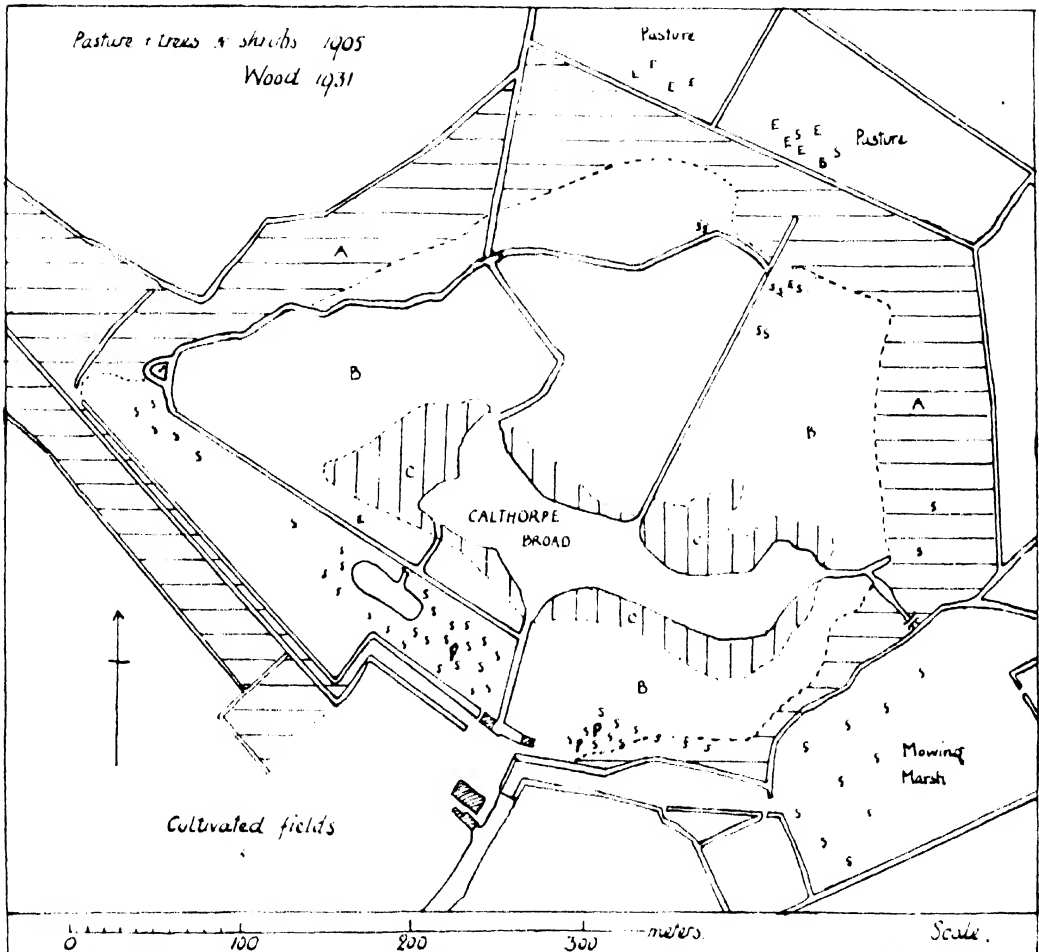
Fig. 3. A map showing the chief vegetation zones round the Broad and distribution of acidiphilous species. *A*, areas shown tree-covered in O.S. of 1905 (i.e. wood); *B*, areas shown bush-covered in O.S. of 1905. The boundary between *B* and *C* is the outline of the Broad as shown in O.S. of 1884 and 1905. *C* is now partly reed-swamp and partly carr, and the outline of the Broad is that of a compass survey carried out by the authors in 1931. *S* = *Sphagnum*, *P* = *Polytrichum*, *E* = *Eriophorum angustifolium*.

ceivably be a natural successional phase following and displacing the carr and subsequently maintaining itself. Naturally the evidence is too slight to be taken as conclusive, but its trend is evident.

(2) *Plant communities.*

It is not proposed to give in this paper any detailed analysis of vegetational composition, but in order to convey a general picture of the communities con-

[1] See **Watt (11)**.

cerned in the above succession and mentioned in the following records of observations on transects and other sites, concise descriptions of the chief plant communities are necessary, and these are given below in as brief a form as possible.

Reed-swamp. On the open water side the reed-swamp is fringed thinly with *Scirpus lacustris*, the extension of which into the Broad appears to be limited by artificial means. Especially at the west end of the Broad, a wide swamp is present dominated by *Typha angustifolia* and *Phragmites communis*, both growing 2·0–2·5 m. tall and excluding almost all other species. At present this reed-swamp is cut annually, the crop being used for thatch.

Intermediate fen and mowing marshes. Following the usage of Miss Pallis the term "intermediate fen" may be employed for a range of communities succeeding reed-swamp, but round Calthorpe Broad these communities are cut from time to time and it seems preferable to use the local term expressive of this, that is, "mowing marsh." An example of the community is typically developed at the west end of the Broad: it is cut, though less frequently than the reed-swamp. The chief constituents are:

Phragmites communis	a.	Scutellaria galericulata	f. -
Juncus obtusiflorus	v.a.	Galium sp.	f.
Carex stricta	a.	Carex paniculata	o.
Potentilla palustris	a.	C. riparia	o.
Hydrocotyle vulgaris	a.	Calamagrostis epigeios	o.
Hypnum sp.	a.	Menyanthes trifoliata	o.
Equisetum sp.	f.	Eriophorum angustifolium	r.
Peucedanum palustre	f.		

In some places on the drier side, away from the Broad, this fen gives place to a community dominated by *Molinia caerulea*. The intermediate fen is readily colonised by bushes of alder, sallow and birch.

On the south-east side of the broad, where the bank slopes more steeply, there is little reed-swamp, and mowing marsh extends to the margin of the Broad. It is similar in composition to that above, but the following species also enter:

Carex panicea	a.	Salix repens	f.
Pedicularis palustris	f.	Schoenus nigricans	o.
Hypnum stellatum Schreb.		Bryum pseudotriquetum Schwaeg.	
H. cuspidatum L.		Aneura pinguis L.	
Lysimachia vulgaris	f.		

In addition to the mowing marshes near the Broad, others occur away from it (see Fig. 3), and they show some rather interesting differences in composition. Thus *Cladium mariscus* is present locally or even abundantly in some of them[1], and *Sphagnum* may occur abundantly. Other common species not so far mentioned which occur here are:

Ranunculus flammula	o.	Carex disticha	o.
Scabiosa succisa	o.	Mentha aquatica	o.–f.
Juncus lampocarpus	o.	Osmunda regalis	o.–f.
Cirsium anglicum	o.	Potentilla erecta	f.

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[1] The absence of *Cladium* from the reed-swamp phase round the Broad may be a result of persistent cropping. It has already been shown that in Cambridgeshire this plant is eradicated by constantly repeated cutting (**2, 3**).

Carr. By increasingly dense bush colonisation of the above communities, a close canopy scrub is formed dominated by *Alnus rotundifolia, Salix cinerea, Betula pubescens* (and rarely *B. alba*). These exist together in varying relative proportions, but the alder is the densest of them near the Broad, and though the alder and birch form almost pure stands, the sallow seldom does so, but plays the part of early colonist, forming a fringe to the advancing carr margin and being killed out as the carr develops to maturity. The sallow behaves similarly to Rhamno-franguletum carr in Wicken Fen, Cambs. Early stages of carr formation are usually marked by dense shade and killing of almost all species of the preceding stage. Under Betuletum, however, the ground may in some cases become densely covered with *Sphagnum* tussocks (see transects 2 *T*, 9 *T* and 10 *T*), in which persist *Potentilla palustris* (f.) (not flowering), *Phragmites communis* (f.), *Osmunda regalis* (o.), and very few other species. The causes underlying the formation of this *Sphagnum*-dominated undergrowth are discussed later. The earlier stages of carr are obviously floating on semi-liquid swamp peat, and the intermediate stages of carr development are generally associated with increasing stability of the ground. This consolidation increases during development from carr into the oakwoods, though in the younger stages of these the ground still quakes slightly[1].

In intermediate carr, the black peat surface is completely bare except for a few bryophytes (*Brachythecium rutabulum* B. and S., *Mnium punctatum* L., *Chiloscyphus pallescens* (Ehrh.) Dum.) and occasional tufts of *Carex riparia, Calamagrostis lanceolata* and *Iris pseudacorus*. At a still later stage the undergrowth becomes denser and has a composition represented by the following list:

Carex riparia	a.	Potentilla palustris	o.
Agrostis alba	a.	Rosa sp.	o.
Iris pseudacorus	f.	Rubus caesius	o.
Carex stricta	o.	R. fruticosus (agg.)	o.
Convolvulus sepium	o.	Solanum dulcamara	o.
Lycopus europaeus	o.	Lysimachia vulgaris	r.
Osmunda regalis	o.		

The trees of the carr reach a maximum height of 5–6 m.

Wood. On the periphery of the older carr there is invasion by oaks and transition to a mixed wood in which *Quercus robur* may in some areas be dominant (e.g. the north-east part of transect 1 *T*). The largest oaks present in the Calthorpe woods are of pioneer form and were probably planted, but very large and well-grown oaks of later generations are also present. Other trees are *Alnus* and *Betula* (both frequent), *Pinus* (planted), and *Fraxinus* (o.).

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[1] It seems probable that when oaks and perhaps birches are present, this process of progressive consolidation is a normal feature of the succession from carr. Where in the absence of oak and birch, alder and sallows dominate the older carr, the field evidence suggests that the ground, far from consolidating and rising, may even sink, exposing the free water surface and leaving the bases of the trees as small islands. The authors are inclined to interpret Miss Pallis's "swamp-carr" as having this origin, and therefore they have not adopted her terminology, which distinguishes between "fen-carr" and "swamp-carr."

Apart from a few small specimens of *Crataegus* and *Salix cinerea*, both often moribund, there is no shrub layer in the well-developed oakwood, where shading out of *Salix* and *Alnus* by the oaks is quite evident. The undergrowth contains:

Phragmites communis	d.	Carex riparia	o.
Rubus fruticosus (agg.)	a.	Cirsium palustre	o.
Agrostis alba	f.	Lychnis flos-cuculi	o.
Convolvulus sepium	f.	Lycopus europaeus	o.
Solanum dulcamara	f.	Rosa sp.	o.
Urtica dioica	f.	Viola palustris	o.
Iris pseudacorus	l.f.		

At 4 *S* (see Fig. 1), at a distance of about 200 m. from the Broad and rather isolated by dykes from the main body of woodland, is a mixed birch-wood with occasional oaks, growing on relatively high firm dry ground. It contains a poor shrub layer of hawthorn and sallow, the ground surface is bare and covered with leaf litter, *Rubus fruticosus*, *R. caesius* and *Holcus lanatus* forming the chief constituents of the undergrowth, with scattered plants of *Dryopteris filix-mas*. In wetter parts of the same wood a relict flora of earlier stages is found, which includes *Phragmites communis*, *Cladium mariscus*, *Agrostis alba*, *Juncus effusus*, *Iris pseudacorus* and *Lysimachia vulgaris*. Since the area is shown in the ordnance survey of 1905 as pasture with scattered trees and shrubs, this wood can hardly be considered as part of the main developmental scheme, although some portions of the woods nearer to the Broad resemble it fairly closely.

III. METHODS.

The preliminary sporadic determinations of the pH of the soil water were made by a rough colorimetric method, but the data quoted in this paper were all obtained with the quinhydrone electrode. This was chosen largely on account of its convenience and rapidity, the compact nature of the apparatus making it particularly suitable for use in a temporary laboratory; it was found possible to use this electrode throughout the work as the reaction is never more alkaline than pH 7·7.

As some of the samples smelled rather strongly of H_2S, it was necessary to check the values obtained by the quinhydrone electrode by other methods whose validity is not affected by the presence in the soil sample of oxidation-reduction systems. Consequently a set of representative samples, some with a strong smell of H_2S, were taken back to the laboratory and tested both colorimetrically and by the hydrogen electrode. It was then found that some of the samples (e.g. the water of the Broad itself) gave no reliable value with the hydrogen electrode, owing partly to a recurrent and rapid poisoning of the electrode, and partly to the removal by the H_2 current of some volatile constituent (not CO_2) altering the pH value. It was then found that such samples contain very slight traces of a substance capable of reducing iodine; this substance was not removed by boiling. This being so, the use of the quinhydrone electrode became suspect, but subsequently a series of samples

were determined both colorimetrically (by Gillespie's drop method) and by the quinhydrone electrode. The values are set out in Table I, where it will be found that the variation is usually within 0·2 pH, which is about the limit of accuracy of the colorimetric method used. It is therefore assumed that for the purposes of this research the quinhydrone electrode is satisfactory; moreover, as the soil water samples are sometimes very turbid or deeply coloured, the use of a colorimetric method without all the resources of a laboratory was out of the question.

A Cambridge-Cole potentiometer was used, and with practice the work becomes rapid, and a reading can be taken in about 3 or 4 min.; in most

Table I.

Sample	Method	pH		Variation
Broads water	Quinhydrone		7·43	
	Col. P.R.	7·3	} 7·30	0·13
	B.T.B.	7·3		
Standing water from mowing marsh	Quinhydrone		6·93	
	Col. B.T.B.	6·8	} 6·8	0·13
	B.C.P.	6·8		
Standing water from mowing marsh	Quinhydrone		6·69	
	Col. B.C.P.	6·5	} 6·50	0·19
	B.T.B.	6·5		
Water from pit under oak	Quinhydrone		6·46	
	Col. B.C.P.	6·7–6·9	} 6·70	0·24
	B.T.B.	6·5–6·7		
Soil under *Sphagnum* and *Polytrichum*	Quinhydrone		6·45	
	Col. B.C.P.	6·4	} 6·35	0·10
	B.T.B.	6·4		
Pit water under *Sphagnum* and *Polytrichum*	Quinhydrone		6·31	
	Col. B.C.P.		6·30	0·01
Soil immediately under *Sphagnum*	Quinhydrone		5·57	
	Col. M.R.	5·4	} 5·6	0·03
	B.C.P.	5·7		
Stamped from leaf litter in a *Sphagnum* area (not under *Sphagnum*)	Quinhydrone		5·10	0·20
	Col. M.R.		4·90	

In the table above the various indicators used are denoted by the contractions P.R. = phenol red, B.T.B. = brom-thymol-blue, B.C.P. = brom-cresol-purple, M.R. = methyl-red.

cases the galvanometer showed a slight drift after the zero had once been obtained, so that the pH often altered by roughly 0·2 pH. This drift is not systematic and could not be correlated with temperature changes, CO_2 loss, etc.: following Olsen, who also noted this phenomenon, we take the first value obtained as giving the pH, though this was always followed until stability was reached.

The soil of the area is almost uniformly wet, even in summer, and most of the samples were taken as water samples from open water, shallow pits or stamped depressions: such water samples were assumed to be in equilibrium with the soil in their neighbourhood, and after standing and decantation gave clear or only slightly turbid solutions suitable for acidity determinations. Water samples were collected in small glass tubes 2·5 × 7·5 cm., which were always first washed out with the water of the sample; ordinary clean corks were used to close them. A relatively small number of soil samples were

taken from the drier parts of the region and these were collected in flat tins
($7\cdot5 \times 10$ cm. diam.): a portion of a sample was afterwards shaken with
water and allowed to stand for several hours: the water was then decanted
into the electrode tube: filtering was abandoned after a few trials as it was
not possible at the time to obtain pure washed filter papers. Values obtained
from soil samples are distinguished in the graphs and tables from those given
by water samples, which are in the majority. All the samples were taken in
the course of a vegetational survey, either of transects, or of selected areas
of special vegetational interest, so that the pH of the soil water, the depth
of the water, the nature and depth of the peat, and the character of the
vegetation can all be stated for each particular region examined.

IV. Results of observations.

(1) *Transects.*

Transect 1 *T*. 134 m. long from the Broad in a north-east direction passing
in succession through reed-swamp, mowing marsh, carr and mixed oakwood.
The typical reed-swamp is modified by cutting in a narrow belt of mowing
marsh in which there is sporadic bush development. The height and distri-
bution of the bushes and trees are shown in the diagrammatic vertical transect
of Fig. 4, and in the belt transect, 5 m. wide, of Fig. 5. It will be seen that
these indicate a transition through a wide belt of carr increasing from 3 to 9 m.
in height and showing invasion, even in early stages, by oaks, which increase
in number and size away from the Broad. The field observations suggest that
the oaks will kill out the other bushes, especially *Salix cinerea*, by shading.
The seed parents of the invading oaks are found in the mixed oakwood ex-
tending from 60 to 134 m. from the Broad. They occur along with *Pinus
sylvestris* (planted), *Fraxinus excelsior* and *Alnus rotundifolia*, all of which are
very well-grown trees reaching a height of 16 m. Most of the oaks were
certainly planted, are of typical pioneer form (F_1), and may have a crown
spread of as much as 22 m.; but there are also numerous second generation
(F_2) oaks which are evidently self-sown. *Sphagnum* occurs occasionally on
the artificially cleared paths through the wood, though not actually on the
transect. The whole length of the transect is underlaid by swamp peat to an
unknown depth determined to be at least 2 m. In the reed-swamp, swamp
peat is continuous to the surface, but in the mature oakwood it is overlaid
by 25 cm. of darker peat in a compact layer. This may be termed "carr peat"
as it is clearly modified by the leaf litter of carr or woods. The carr peat
increases in thickness from the early stages of carr formation up to the outer
margin of the wood. The average height of the peat surface above the water-
table increases gradually from below zero in the reed-swamp to 40 or 50 cm.
at the outer margin of the wood. The reed-swamp is floating on open water
or very soft swamp peat: in the carr the ground quakes considerably and this

persists markedly into the middle of the oakwood (Schwingmoor, see p. 259). The acidity relationships are shown in Fig. 4: acidity increases regularly with increasing distance from the Broad and height of the peat surface above water-level, reaching pH values as low as 5·4 for water samples and 4·6 for surface soil samples.

Transects 3 T and 2 T. These transects can be considered together, since the one continues into the other and they have been shown together in Fig. 6. Their position and direction can be seen in the figure.
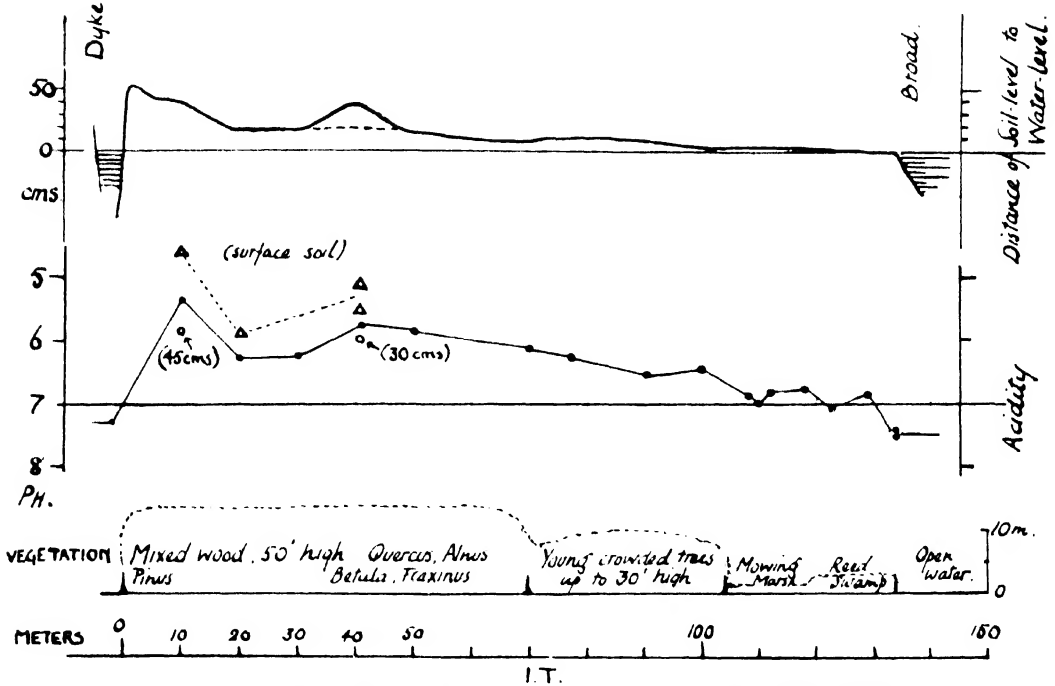
FIG. 4. Observations made along transect 1 T. The acidity values unless otherwise stated are those of water samples.

3 T commences in reed-swamp dominated by *Typha* in which the soil surface is some centimetres below water-level. At 10 m. the vegetation changes to that of mixed fen dominated by *Carex* and *Juncus* and invaded by scattered small bushes of *Alnus, Betula* and *Salix*; here the soil-level is approximately 2–3 cm. below water-level. Progressively the frequency and size of bushes increases up to 4 m. at the edge of the dyke. All the ground quakes and swamp peat underlies the whole to more than 2 m. depth. The soil reaction is only slightly less alkaline than the Broad.

2 T. A transect of 85 m. which commences at the edge of the dyke in young carr of *Salix, Alnus* and *Betula* 5 m. high; this carr extends over the greater part of the transect. At 15 m. *Sphagnum* begins to appear, increasing in density, at 40 m. covering more than half the ground. At 55 m. *Q. robur* first occurs and at 66 m. there is transition from carr to a wood with *Quercus*

and *Betula* 8–9 m. high with a dense canopy and little undergrowth: here the *Sphagnum* is absent. The soil is 5–10 cm. above the water table throughout the transect, though there are high raised banks at each end of it. The lake peat is more than 2 m. thick at the Broad and underlies the rest of the transect at a depth of at least 1 m., except possibly under the wood.
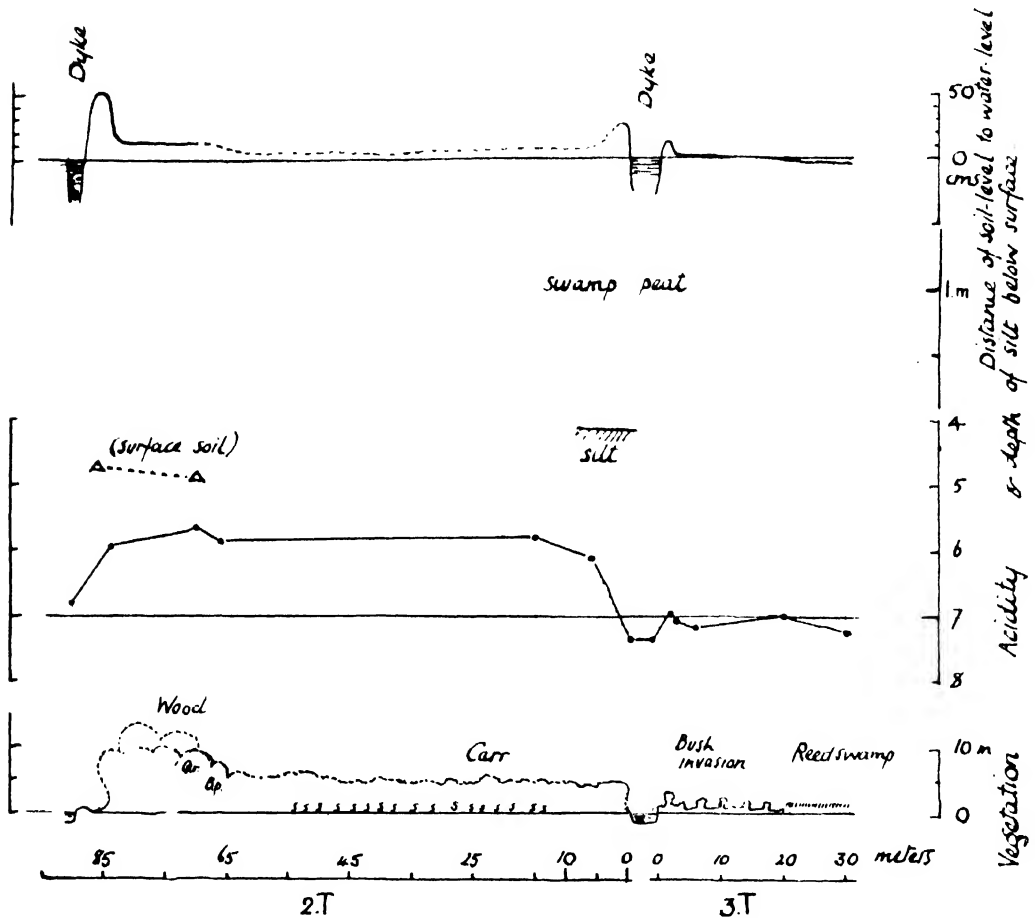
Fig. 6. Observations made along transects 3 *T* and 2 *T*. The acidity values unless otherwise stated are those of water samples.

In contrast to the soil water of 3 *T* all the water samples of 4 *T* show a uniform and fairly high acidity, the *p*H lying between 6·1 and 5·7. The *p*H values of the soil samples from the wood are from 4·9 to 4·7.

Transects 5 *T*, 4 *T*, 12 *T* may best be considered together, since they make a consecutive series running outwards from the Broad (Fig. 7).

5 *T* begins at the Broad margin and is entirely within a reed-swamp containing only *Phragmites* and *Typha* 2–2·5 m. tall where the soil surface is 15 cm. below water-level. The *p*H of the soil water differs little from that of the Broad (7·2–7·3).
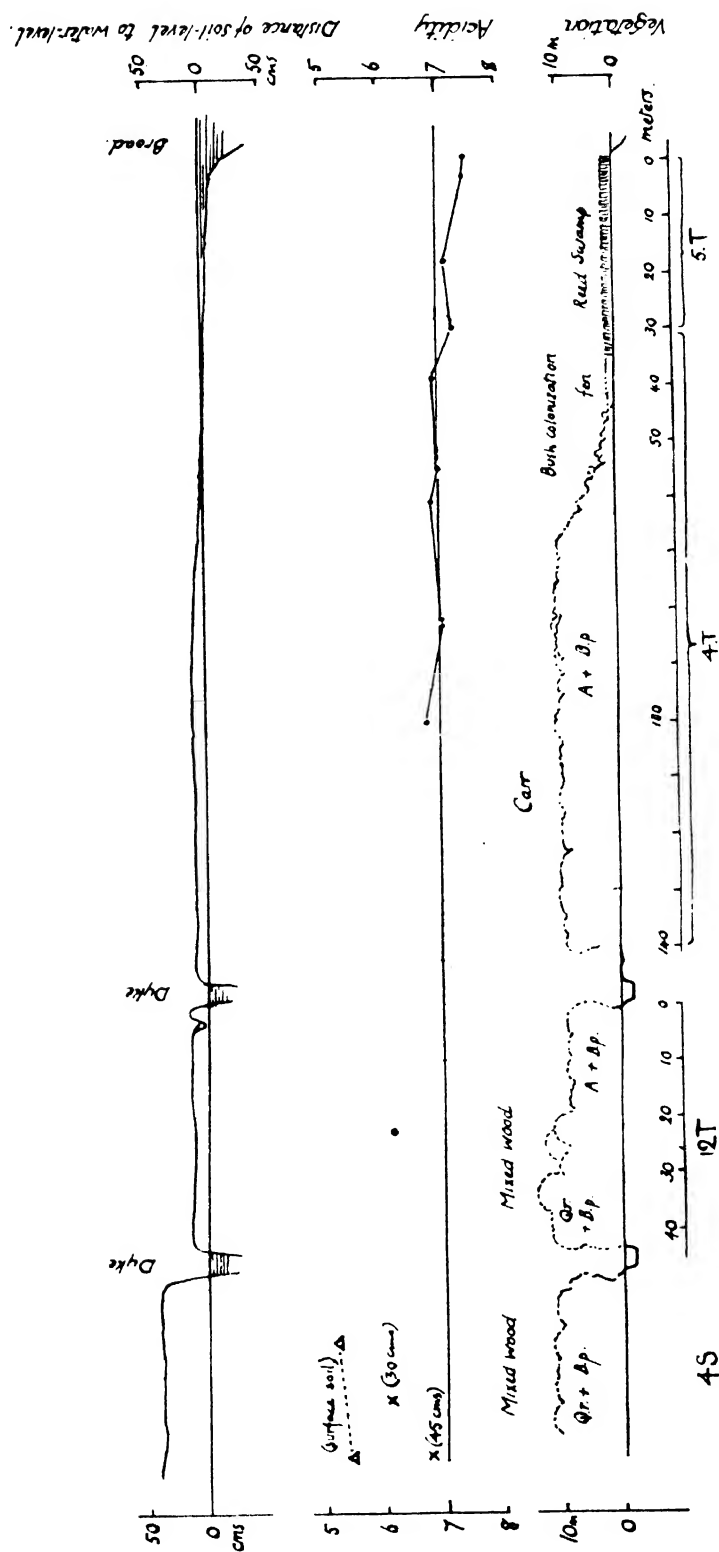
FIG. 7. Observations made along transects 5 T, 4 T and 12 T and on site 4 S. The acidity values unless otherwise stated are those of water samples.

4 *T*. The reed-swamp of 5 *T* continues into 4 *T*, but at 45 m. from the Broad is replaced by mixed fen dominated by *Carex* and *Juncus*. Bush colonisation begins at 46 m.: closed carr is established at 60 m., and this increases in height to 9 11 m. The ground rises gradually to not more than 10 cm. above water-level and the reaction is approximately neutral or just on the acid side of neutral.

12 *T*. On the far side of the dyke is found a rather mixed wood, with *Betula, Alnus, Quercus* (11–13 m.) and occasional *Fraxinus* (4·5 m.), with some *Salix* and *Crataegus* in a dying condition. The soil is here rather higher than in 4 *T*. The single soil water sample gave a value of 6·1. Still further from
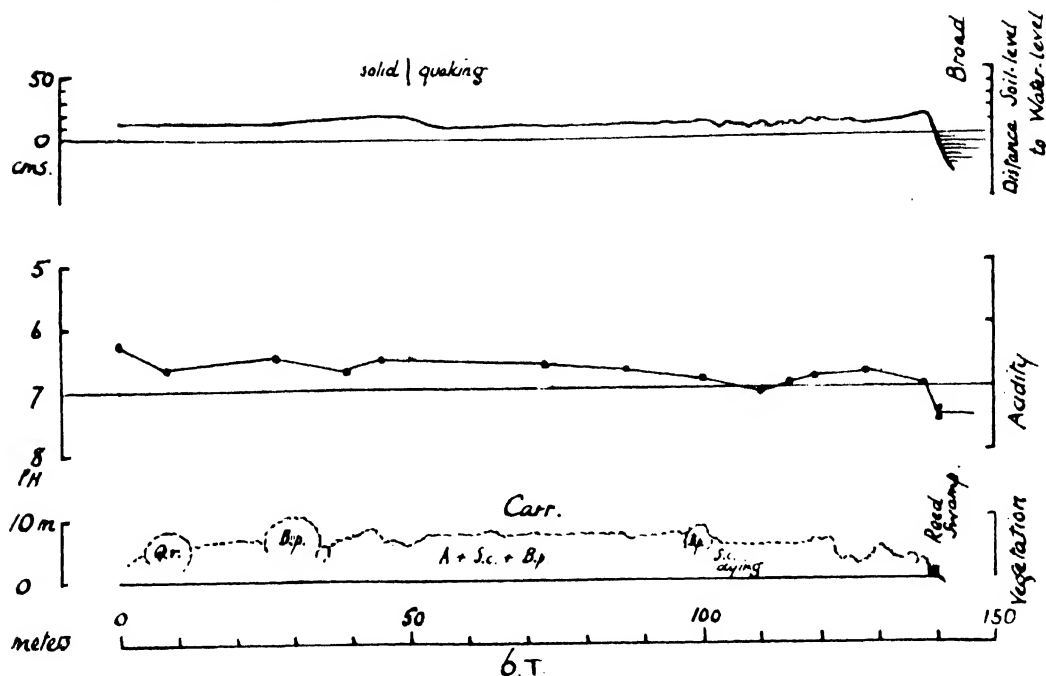
Fig. 8. Observations made along transect 6 *T*. The acidity values are those of water samples.

the broad in the same north-west direction and separated by another dyke is an extensive oak-birch wood 10–12 m. high, possibly in part planted. The soil level is 40 cm. above water-level, though the wood is on peat at least 3 m. deep. Surface-soil samples gave *p*H values of 5·2 and 5·4.

Transect 6 T is about 140 m. long and runs north from the edge of the Broad (Fig. 8). Young carr, 3 m. high, is found almost on the margin of the Broad and soon increases in height to 5 m. Up to 90 m. along the transect there is a peculiar carr dominated by *Alnus, Betula* and *Salix* growing ("floating") on very soft quaking peat: there is little ground vegetation, and locally *Salix* appears to be dying out: the ground-level is variable. After 90 m. the soil remains at a consistently higher level above the water table and the ground is more stable. Isolated patches of living *Cladium* point to

the derivation of the carr from fen. Here the carr is taller and more stable and contains very large pioneer forms of *Betula* and *Quercus*, as well as younger oaks: the older trees are locally killing out the bush layer.

This transect comprises a wide belt of carr all in about the same state of development, and the ground-level rises very slowly to about 20 cm. above water-level. The soil reaction is increasingly acid (with a few local variations), although the increase is very gradual, and the lowest *p*H value reached is 6·2.

Transect 8 T extends to 52 m. from the Broad in a south-east direction, passing through mowing marsh and carr (Fig. 9). The mowing marsh extends to the edge of the Broad and shows stages of increasing density of bush colonisation passing away from the Broad. Further along the same line the carr becomes more mature and open, increasing up to 6–9 m., and showing invasion by a few scattered oaks, probably self-sown from pioneers planted on the dyke bank. Under the old carr there is a thin layer of carr peat; below this and along the whole transect swamp peat extends to a depth of 165–180 cm.: below this is white silt. The average height of ground-level above water-level increases along the transect from about 8 to 15 cm. The ground quakes appreciably along the margin of the Broad and progressively less away from it, and the soil-water samples are slightly acid, their *p*H values lying between 6·3 and 6·8. Characteristic acidiphilous species are lacking.

Transect 10 T is 81 m. long, passing from the Broad almost due south (Fig. 9). The first 26 m. are mowing marsh sporadically colonised by bushes. Young carr about 2 m. high occurs densely from 26 m. and increases in height to about 6 m. at the other end of the transect. From 14 m. onwards the ground is almost completely covered with deep tussocks of *Sphagnum* intermixed sparsely in places with *Polytrichum commune*. Swamp peat underlies the whole transect, but the underlying silt rises uniformly from a depth of 2·1 m. at the Broad margin to 25 cm. at the other end of the transect: shallow carr peat occurs at the other end of the transect. The height of the peat surface above water-level is roughly constant at from 5 to 10 cm., rising somewhat at the end away from the Broad, where, however, *Sphagnum* tussocks make the estimation peculiarly difficult. The acidity of the soil water increases steadily away from the Broad to a value of *p*H 5·6 at 80 m. where water squeezed from the surface soil showed a *p*H value of 4·9 and that squeezed from the *Sphagnum* tussocks themselves *p*H 4·2.

Transect 9 T resembles transects 8 and 10 and is in all ways intermediate between them (Fig. 10). It lies about midway between them and also runs south from the edge of the Broad through mowing marsh and carr of increasing age and height. The white silt below the swamp peat rises from a depth of 1·95 m. at the margin of the Broad to 0·95 m. at the south end. Abundant *Sphagnum* is limited to a short portion of the transect under the tallest carr at the end furthest from the Broad. The peat surface is the same general height above the water table as before, and the soil-water acidity
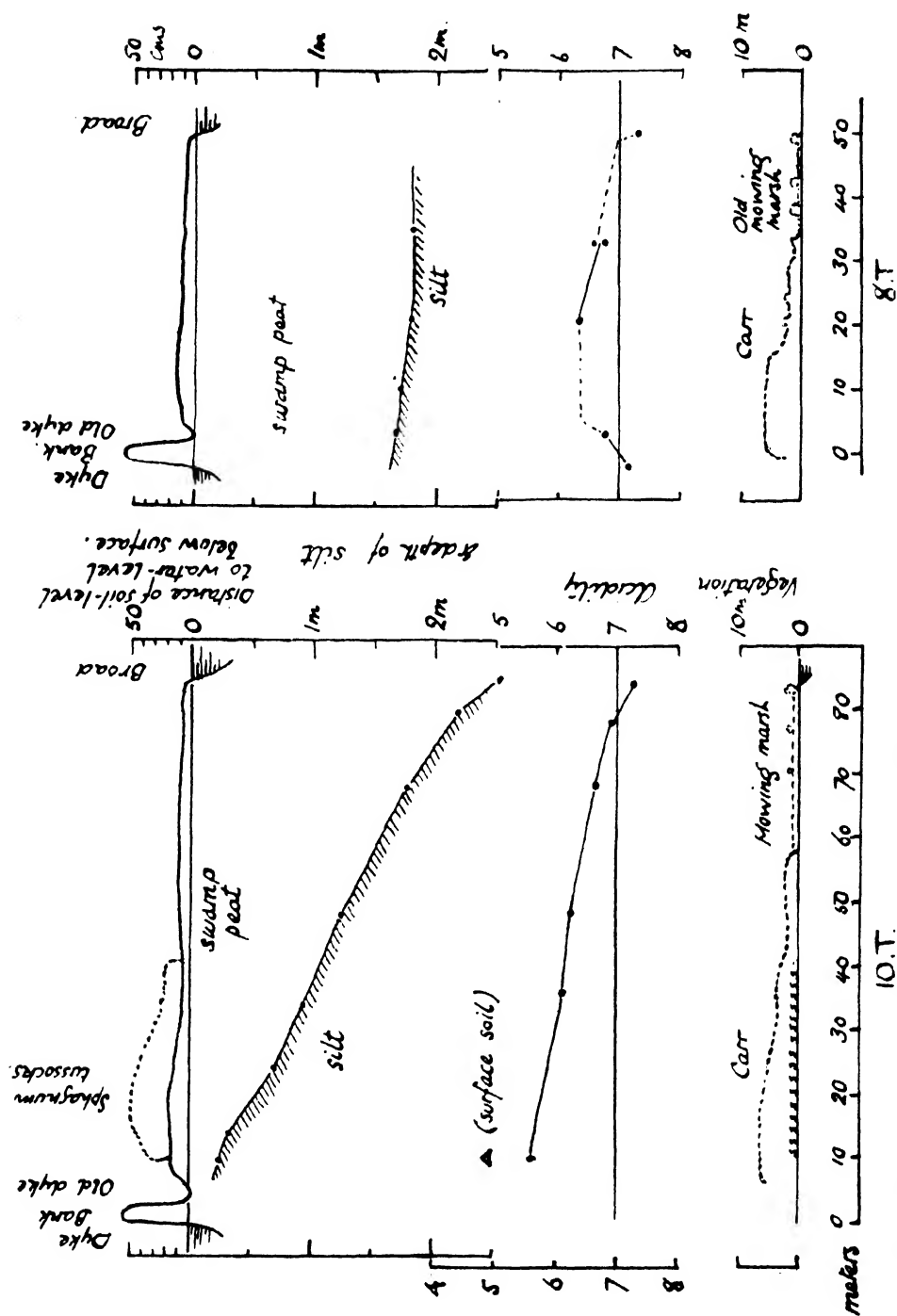
Fig. 9. Observations made along transects 8 *T* and 10 *T*. The acidity values unless otherwise stated are those of water samples.
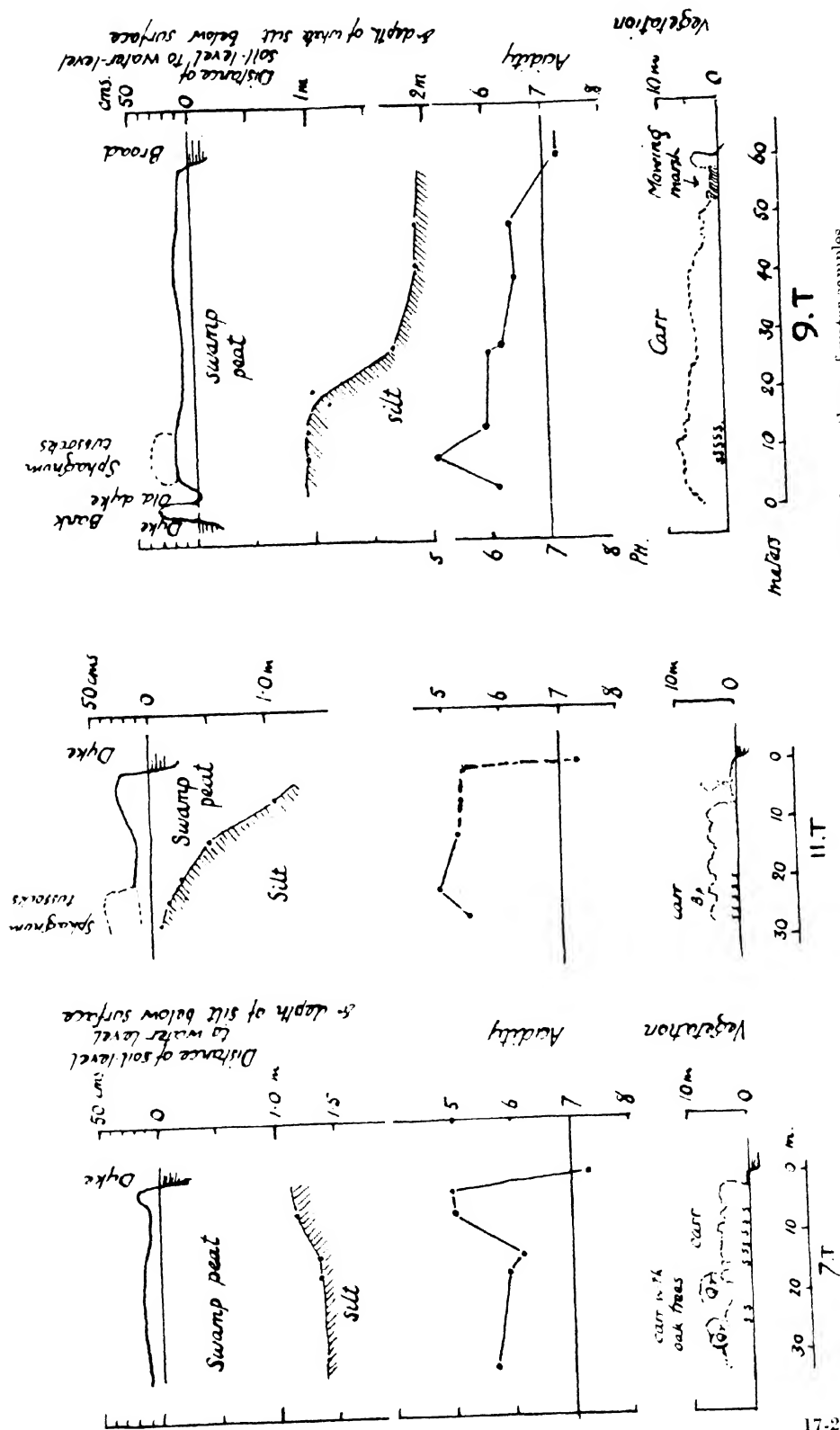
Fig. 10. Observations made along transects 7 T, 9 T and 11 T. The acidity values are those of water samples.

17·2

also rises gradually along the transect away from the Broad to values of
about pH 6·0 in the region with no *Sphagnum* and to pH 5·1 in the parts
with *Sphagnum*.

Transects 11 *T and* 7 *T* (Fig. 10). These transects, together with 2 *T*, occur
in the area forming the south-east margin of the Calthorpe basin where it
abuts on the upland. This area is also separated by a dyke and a consolidated
bank from the vegetation immediately surrounding the Broad. Its situation
and drainage relations may have markedly influenced the character of the
area. Transect 11 *T* passes through fairly uniform carr of *Alnus, Salix cinerea*
and *Betula pubescens*, about 5 m. high, occasionally reaching 6 or 7 m. Young
Quercus robur of the same height is frequent. *Sphagnum squarrosum* and
S. fimbriatum occur densely and cover the greater part of the ground with
deep tussocks which have living *Sphagnum* about 15–20 cm. deep overlying
about 20 cm. of *Sphagnum* peat. This rests on swamp peat which extends to
the white silt. The surface of the white silt slopes steeply to the north,
evidently forming the old southern margin of the Broad. The soil, apart from
the dyke bank, is from 10 to 15 cm. above the water-table, and the soil water
has pH values of 5·0–5·5.

7 *T* is similar in most respects to 11 *T*, being covered by carr of similar
character with abundant *Sphagnum* on the ground, but, on the side away
from the Broad, the carr contains numerous oak trees 8 or 9 m. high. The
silt below swamp peat lies at a fairly uniform depth of 1·2–1·4 m. and the
peat surface is 10–15 cm. above water-level. The pH values for the soil water
lie between 5·0 and 6·2.

Transect 13 *T* (Fig. 11). This transect, which is about 90 m. long, lies
entirely in a mowing marsh on the south side of the Broad and some distance
from it. The area is dominated by *Phragmites* and *Juncus obtusiflorus*, but
Potentilla palustris and *Sphagnum* tussocks are also very abundant. The swamp
peat underlies the transect and the white silt below it rises from 2 m. depth
at the north-west end to 0·75 m. at the south-east end. The soil-level falls
from about 20 cm. above water-level at the north-west end of the transect
to about 10 cm. at the south-west end, but the soil acidity increases to the
south-west, i.e. away from the Broad, reaching a value as low as pH 5·4.
It is very interesting to find in this marsh a vegetation exactly like that
typical of alkaline peat (see pp. 242 and 243) but containing also *Sphagnum* and
having markedly acid soil.

(2) *Separate sites.*

1 *S* lies on the very southernmost margin of the Calthorpe peat area, where
the white silt is covered by only 45 cm. of peat, the greater part of which is
soft brown swamp peat. Young *Betula* carr 4 or 5 m. high occupies the area
and the ground is densely covered with *Sphagnum* tussocks containing here and
there a little *Polytrichum*. The surface peat showed pH values of 5·09 and 5·57.

2 *S*, though under similar vegetation and not far distant from 1 *S*, differed from it in the much greater depth of swamp peat overlying the silt, at least 1 m. and probably a good deal more. *Sphagnum* was also present here and water squeezed from the surface peat under *Sphagnum* gave pH values of 4·97 and 4·99, the surface peat not under *Sphagnum* giving pH 5·10. This is especially striking since the site is within 6 m. of a large lily pond connected with the Broad and itself containing water of pH 7·05.

3 *S* is situated very near transect 7 *T* and is covered with carr heavily invaded with thin F_2 oaks up to 8 m. high. The especial interest however
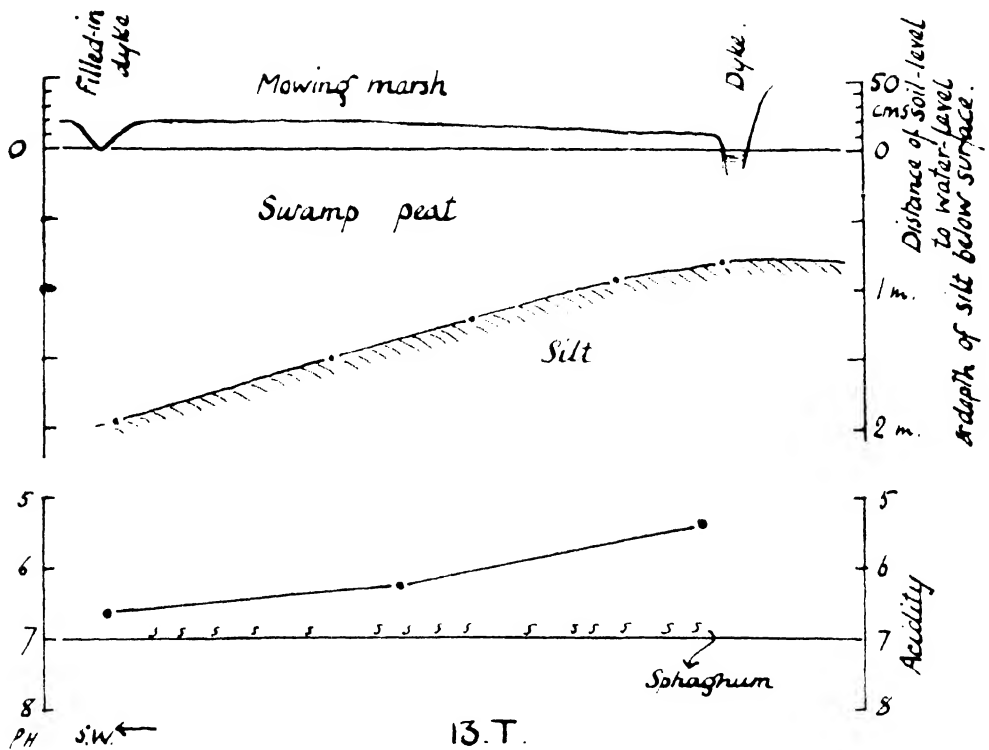
Fig. 11. Observations along transect 13 *T*. The acidity values are those of water samples.

lies in a dense undergrowth of tall, healthy *Cladium*. The soil level is 26 cm. above water-level. Black peat 6 cm. deep overlies swamp peat, which covers the white silt to a depth of 190 cm. The water from a shallow pit dug here showed pH 5·52, but the surface leaf litter showed 3·59.

4 *S*, see description of 5 *T*, 4 *T* and 12 *T*.

5 *S and* 6 *S*. These sites occur in two small clearings, in the middle of well-developed carr, which are used as mowing marshes. They have the vegetation described before, dominated by *Phragmites* and *Juncus obtusiflorus*, with locally abundant *Cladium*, and generally abundant *Molinia*. It is a vegetation generally typical of alkaline peat but it contains scattered tussocks

of *Sphagnum* and occasional *Eriophorum angustifolium*. Also small plants of
Osmunda regalis occur frequently. The soil-level varies from 5–8 cm. to
12–15 cm. above the water-level, and no bottom could be found to the swamp
peat underlying the areas; it was certainly deeper than 2·8 m. Soil-water
samples from the surface showed a *p*H value of 6·40, and from a shallow pit
of 6·23 and 6·74. Water squeezed from the surface peat layer gave values of
*p*H 5·80, 5·89, 6·32 and 6·50, and that squeezed from the *Sphagnum* tussock
itself *p*H 4·30.

7 *S*. Under the canopy of a large oak 6 m. high, which formed a raised
"island" in the level peat of the surrounding old carr, the leaf litter of the
surface layer showed *p*H 5·33. The water table was 16–18 cm. below. Water
from pits dug down to water-level at different points under the oak tree gave
*p*H values of 6·15, 6·26 and 6·52.

8 *S and* 9 *S*. These are sites just outside the tall border of woodland sur-
rounding the Broad and they are in rough meadow pastured by horses and
cattle. In them, *Juncus obtusiflorus*, *Molinia caerulea* and *Carex panicea* are
co-dominant, though *Eriophorum angustifolium* is locally dominant in the
hollows. Numerous fen species occur with these plants and in 8 *S* there are
also large *Sphagnum* tussocks. The peat is firm and compact though it is still
swamp peat except the surface layers. The water-level below the *Eriophorum*
and *Sphagnum* in these areas is 28–35 cm. below the soil surface. The surface
water under *Eriophorum* in a dyke in 9 *S* gave *p*H 5·63, the soil water in a
pit near by *p*H 6·02, and the swamp peat from 60 cm. depth in the same
place *p*H 6·09. The peat just below *Sphagnum* in 8 *S* showed *p*H 4·90.

10 *S* is a site not indicated on the map. It lies on the extreme north-east
margin of the Calthorpe basin where the underlying silt rises to cultivated
land beside Waxham cut. It consists of a large area (perhaps 5000 sq. m.) of
almost pure *Eriophorum angustifolium* which contains very local *Juncus effusus*,
occasional *Phragmites*, and scattered small tufts of *Sphagnum*. The meadow,
though possibly not all the area, is cut for hay. On the meadow side nearest
the Broad white silt lies at 111 cm. from the surface, and it rises gradually
to within 20 cm. of the surface where the *Eriophorum* is farthest from the
Broad. Swamp peat overlies the silt. The water content of the peat is low
and water soaks very slowly into newly dug pits. Water from such a pit gave
a *p*H value of 4·31 and water squeezed from a *Sphagnum* tuft a value of 3·91.

11 *S* is the mowing marsh described under transect 13 *T*. Samples of
various kinds were taken in addition to those on the transect. The surface
water in an area with *Sphagnum* tussocks gave *p*H 6·05, and the water in a
shallow pit dug where *Sphagnum* and *Cladium* occurred together gave *p*H 6·15,
the surface soil at this point giving *p*H 5·12.

(3) *Distribution of acidiphilous species.*

The map (Fig. 3) presents most of the important data with respect to the distribution of acidiphilous species on the area round the Broad. Most of the localities shown have been mentioned in the description of transects and separate sites. The map is not intended to be regarded as necessarily including all existing sites for acidiphilous species though it is believed to be fairly comprehensive. The *Sphagnum* sites showed the following species[1]: *S. fimbriatum* Wils. LMS., *S. squarrosum* Pers., *S. subsecundum* Nees, *S. acutifolium* Ehrh. var. *subnitens* Dix. *Mnium hornum* L. was found occasionally on tree stumps under carr in the region of 1 *S* and 2 *T*, though never on the peat surface itself, the mode of occurrence strongly recalling the cases quoted by Domin (**1**) from the Tatra Mountains of decomposing stumps and trunks as points of support for the invasion of calcifugous elements into a calcareous region. Occasionally *Polytrichum commune* L. was found growing among the *Sphagnum* tussocks and this also is shown on the map. The Sphagna are all "low moor" species, and the only angiospermous species shown on the map, *Eriophorum angustifolium*, is generally known to occur in similar habitats.

It will have become clear from the preceding data that the indications of soil acidity given by the presence of these species have been uniformly confirmed by the electrometric measurements of soil acidity, although the acidity developed is seldom extreme and may in some cases be very slight (e.g. *Eriophorum* at the south end of 3 *T*, which grew in a region where the soil water was practically neutral).

It is important to notice that the areas bearing acidiphilous species (*a*) occur on all sides of the Broad, and (*b*) are not found except at a considerable distance from it. The first point indicates that their presence (and soil acidity) is not merely due to proximity to the sandy upland margin of the peat basin with only a shallow depth of peat (as could be said of some of the *Sphagnum* areas on the south side of the Broad), for the peat basin extends far to the north of the area shown on the map and the peat depth is certainly over 2·5 m. The second point indicates that soil acidity develops naturally and progressively with distance from the Broad, a fact already suggested by the transects.

The occurrence of the acidiphilous species is naturally subject to control by factors other than that of soil reaction, and we may expect that of the dominant vegetation to be important. In this connection it should be noted that *Sphagnum* occurs in young carr (especially Betuletum), in pathways in oakwood and old carr, in mowing meadows along with *Phragmites, Juncus* and species of *Carex*, in mowing meadows with *Eriophorum*, and in rough pasture with *Molinia* and *Eriophorum*. Some degree of shading (and roughly corre-

[1] For the determination of these moss species and also of many more not here referred to, the authors are greatly indebted to Mr P. W. Richards.

sponding protection from desiccation) is afforded by all these habitats, but the denser shade of mature carr and of the tall uncut undergrowth in the oakwood appears to exclude *Sphagnum*.

It is possible that the great abundance of *Sphagnum* in the young carr to the south of the Broad is due in part to the causes suggested above, that is nearness to the upland and shallowness of the peat, and in part at least in the south-east part of the area to protection against direct flooding from the Broad given by the high bank of the long straight dyke running about east-north-east. It is clear, however, that such an explanation cannot entirely hold for the south-west of the area where no dykes or banks intervene between *Sphagnum* sites and the Broad.

Despite the local variations in density there seems no escape from the general conclusion that the acidiphilous species grow where they do primarily because these sites are sufficiently distant from the Broad and on peat grown sufficiently above reach of alkaline flood waters to become acid in reaction.

V. Conclusions and Discussion.

From the data given in the foregoing section, conclusions can be drawn as to the development of soil acidity in the Calthorpe area, in relation to the course of vegetational succession and the progressive invasion of the Broad and to the increasing height of the ground-level above the water-table, which goes with the succession.

The ground appears to be acid just in so far as it is removed from the influence of the ground-water of the Broad and the dykes in easy communication with it. The low-lying reed-swamp, fen or carr close to the Broad may have a soil water which is only slightly acid, but further from the Broad the ground develops marked acidity and supports characteristic acidiphilous species. Lateral distance from the Broad and vertical height of soil-level above water-level are the primary factors in protecting these areas from the effect of the alkaline Broad water, and in general they run parallel with one another and with the main course of vegetational zonation and succession. Thus the reed-swamp is lowest in level nearest the Broad and is in the earliest phase in the above-water succession. The carr dominated by bushes is the next successional stage: it occupies a zone further from the Broad and has a higher soil-level. The wood, which possibly represents the climax phase of the prisere, forms the outermost zone round the Broad and has a soil-level highest above Broad-level.

In relation with this sequence of controlling factors there is a progression in the soil acidity from the Broad outwards; and, in general, the most advanced communities are the most acid. As would be expected however, local conditions of various kinds modify this progression: thus, wherever the depth of peat is slight or where areas are separated from the Broad by high banks, flooding may be expected to take place less readily and acidity to be more

marked. This may in part explain the very prevalent high acidities along the southern margin of the Calthorpe area.

The leaf litter from trees forms acidic humus (as for example especially below beech, see Watt and Tansley (**12**)). This might enhance the acidification of the soil in later stages of the succession, but that it is by no means an essential factor is shown by the development of Sphagneta and Eriophoreta on completely treeless mowing marshes and meadows, and by the gradual transition from alkalinity in much earlier phases of the vegetational succession.

The logical outcome of these results is that *the formation of acidic peat and its colonisation by acidiphilous species must be regarded as the normal result of vegetational succession from some, at least, of the originally alkaline Broads of Norfolk.* The occurrence of Sphagna and other acidiphilous species is not interpretable in terms of local extensions of upland communities, but as an indication that a certain stage of normal soil development has been reached.

The suggestion that progressive soil acidification might be the result of normal developmental processes has, of course, been made previously: in a footnote to Miss Pallis's descriptions of Broadland Sphagneta in *Types of British Vegetation* (**4**), Tansley has added: "Similar (fen) associations are well known to pass regularly into moor on the continent, and there is evidence from the peat records that they have done so in the past in this country." In the same book, Munn Rankin describes the evidence from succession of peat strata that the lowland moors of Lonsdale in North Lancashire have been derived from fens. It will, however, be more satisfactory to compare the stages in the Calthorpe area with existing types of similar vegetational succession such as those described by Steffen for North-east Germany (**10**), and by Pearsall for the Lake District of this country (**5**). Steffen has described the following sequence of communities from open water in the delta of the River Memel in North-east Germany. Free-floating and rooted aquatics of the open water give place to reed-swamp, which by progressive interlacing of roots and rhizomes forms a platform of increasing strength floating upon the lake mud or lake peat. This is the "Schwingmoor" which rocks and bends when walked upon[1], and which by continual aggregation of material eventually consolidates the underlying peat and so establishes firm "Standmoor." This, where the ground water has a high concentration of mineral salts, is "Stand-flachmoor," which becomes shrub and tree covered to give alder wood, "Erlenstandmoor." With increasing growth of peat above the level of the ground water leaching of mineral salts begins, and with it vegetational changes; especially important is the entry of Sphagna under suitable conditions. Birch and pine also enter, and a so-called "Mischwald-Zwischenmoor" is formed. This passes into pine (or birch) "Zwischenmoor" with a very limited and characteristic acidiphilous ground vegetation. Finally, if conditions of humidity, rainfall, etc., are favourable, continued development of

[1] See also **Weaver** and **Clements**, p. 72 (**13**).

Sphagnum peat leads to the ultimate replacement of this by "Hochmoor" in which the only trees are a few dwarfed pines. Under conditions of lower rainfall this climax may not be reached, and development is arrested in an earlier stage. It can be seen that the sere embraces the entire transition from Flachmoor to Hochmoor with progressive edaphic modifications, from the alkaline open water rich in mineral salts to highly acid *Sphagnum* moor poor in salts.

Pearsall (**6**) in 1918 suggested a scheme for the classification of aquatic plant communities which was based on the principle that (*a*) open water aquatic plant communities, (*b*) fen, and (*c*) moor were phases of a unit succession, and though this was based essentially on observations in the Lake District, Pearsall considered the principle to apply to all parts of this country, quoting supporting evidence from descriptions of areas in Cheshire, Somerset and the Norfolk Broads. Of the last he says: "local conditions (low rainfall and rich soil waters) extend the importance of the *carr* stage, while cultivation, drainage and especially climate limit the development of moor." From his work on the vegetation of Esthwaite Water he concluded "that moor can be regarded as a climatic formation is proved by its permanence in the western parts of the British Isles. Both present observations and the peat evidence show that the hydrarch succession does not, as in the U.S.A., pass into forest."

It is not difficult to accept the view that in the west of England, moor is indeed a climatic climax community, and it may certainly be associated with high rainfall, or more exactly, perhaps, with high values for the rainfall/evaporation ratio. The succession to deciduous woodland in North America, presumably under conditions of lower rainfall or lower rainfall/evaporation ratio is at least equally well attested, so that we may well ask what intermediate vegetational development between the two occurs in regions of intermediate precipitation and evaporation. In Esthwaite Water, Pearsall describes an early formed carr dominated by *Salix cinerea* as the only phase in the succession controlled by phanerophytes and this quickly gives place to Molinietum which passes into moor. As we have seen, he considers that East Anglian conditions extend the importance of the carr stage. Our preliminary observations suggest that the stage may indeed be extended so far as to give for a long time, if not permanently, a community of deciduous woodland. If this is indeed the case, the gradient of rainfall and evaporation from west to east across England may really be effectively determining two types of climatic climax, moor in the west and deciduous wood in the east. At the same time, although we may deny the likelihood of the sere reaching the same climax of moor in the east, as in the west of England, the present results do show edaphic processes of exactly similar nature at work; that is, progressive accumulation of peat to the point of the complete filling in of open water, and then leaching and progressive acidification of the surface peat, with a corresponding establishment of some characteristic acidiphilous

species where other conditions are suitable. The Calthorpe area (and probably the Broads region as a whole) may indeed be looked upon as intermediate between the type of succession in which Sphagna dominate the later stages of development and determine the absence of woodland and establishment of a Hochmoor climax, and the type of succession from which Sphagna are absent and which ends in a climax of deciduous woodland. In this area Sphagna appear abundantly in special local conditions, but do not affect the trend of the succession to a climax of deciduous woodland.

There is in the Calthorpe area no evidence as to whether the oakwood climax approaches that of naturally drier soils in this country (such as have been described by Salisbury (8)) or whether they reach some stable form intermediate between such oakwoods and moors (perhaps an acid birch-oak heath type of wood). We hope that future work may be able to elucidate the point.

VI. Summary.

1. Calthorpe Broad is a northerly part of the Norfolk Broads system. It shows a concentric arrangement of plant communities round it in the shape of (a) reed-swamp, (b) carr (scrub), (c) woodland, and there is evidence to show that these are developmental stages of a primary hydrarch succession which is still going on. Some communities subject to crop-taking ("mowing marshes"), and some to grazing are also present.

2. The carr is dominated by alder, sallow and birches, and the woodland by oaks and birches, with less frequent alders, ashes and planted pines. The general character of the vegetation is that of "Niedermoor" which is in keeping with the alkaline nature of the water of the Broad, and with current conceptions of the status of the vegetation of the Norfolk Broads. At the same time, several acidiphilous species are found at Calthorpe, and their distribution suggests that they have appeared in relation to a naturally developed acidity of the growing peat.

3. Observations of vegetation, of the height of the peat above water-level, and of the reaction of the soil (determined by the quinhydrone electrode), were made along transects radiating from the Broad in various directions and also in separate sites. The results show that, throughout the vegetational succession, as (a) the ground-level rises and (b) distance from the Broad increases, so the soil acidity increases. Those communities lowest and nearest the Broad have approximately neutral soil, and those away from it have pH values as low as 5·0. Extensive *Sphagnum* undergrowth may occur in carr, in mowing marshes and in pastures, but it does not appear to affect the development of the succession to the mixed oakwood climax.

4. It is concluded that progressive soil acidification and the corresponding establishment of acidiphilous species must be regarded as the normal result of vegetational succession. In view of this the succession in the Calthorpe

area is compared with those described by Steffen for North-east Germany, and by Pearsall for the Lake District of this country, both of which lead to the establishment of Hochmoor. It is suggested that the Broads area is possibly intermediate between these types and those in which deciduous forest is the unmistakable climax community.

The authors wish to express their sincere thanks to Dr Robert Gurney, who has not only given them the fullest access to his property at Calthorpe, but who has interested himself personally in the work and facilitated it where possible.

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FURTHER OBSERVATIONS ON THE SALTMARSH AT HOLME-NEXT-THE-SEA, NORFOLK

By V. M. CONWAY.

(With Plate XIII, one Figure in the Text and one Folding Map.)

THE saltmarsh and sand-dunes at Holme-next-the-Sea have been under investigation by members of the Cambridge Botany School from time to time during the last twenty years. The accompanying map of this area, made in August, 1931, is intended for comparison with the one made in 1913 and published in 1915 (**1**). Accurate methods of survey were not available, but it is estimated that 3 per cent. is the maximum error to which the measurements are liable. No Ordnance Survey of the district has been published since 1905, so that it has not been possible to check the mapping by this means. The posts I, III, IV, V and VI of the 1913 base-line were found and the position of II measured out. By a geometrical method perpendiculars to the base-line were made through each post and a line was marked out in I-II S parallel to the base-line and 4 chains south of it, and a similar one in II-III S, 2 chains south of the base-line. The shingle-fan in IV-V N was measured across its greatest length and breadth. The vegetation was mapped by making notes of the type of association in each chain measured along these lines. In mapping the intermediate regions use was made of the fact that the main drainage channels had altered so little that their general course could be adopted from the 1913 map, while slight alterations could be mapped by eye. Pools and small channels were also mapped along the transects and as accurately as possible by eye in the intervening regions, except in the most southern area where they were too numerous to be dealt with. The accurate representation of the shape and size of the pools cannot be guaranteed, but it is hoped that every pool over a yard in length has been indicated so that a comparison of the numbers at least is possible.

No attempt was made to re-map the vegetation on Gore Point and on the south bank, as it seemed to have changed little since 1913.

The following are the most important points brought out by a comparison of the two maps.

I. TOPOGRAPHICAL CHANGES.

The process of erosion observed by Wadham (**2**) and Peace (**3**) has continued. It is estimated that since 1913 Gore Point has been eroded back 44 yards in a south-east direction. A very high spring tide which occurred during the period of observation came right up to the fixed dunes and in places undercut them so that as much as a yard of the fixed *Ammophila* dune

was broken away. In the region III–V N a wide breach was made between July, 1930 and July, 1931 (see Pl. XIII, phot. 1); the spring tide flows over it and if the border of *Suaeda fruticosa* dies, it seems likely that winter storms may force a deeper entry at this point. The breach is reported to have widened by November, 1931. The spring tide also washes over the shingle region in II–III N and it appears at present that before long all the dune ridge north of III will be broken away. Should this happen, the marsh will be open to the force of winter storms and there may be a risk of damage to the bank on the south which protects reclaimed land. The diagrammatic scale-map (Fig. 1) illustrates the extent of the erosion (cf. (**2**), Figs. 1 and 2, and (**3**), Fig. 1).
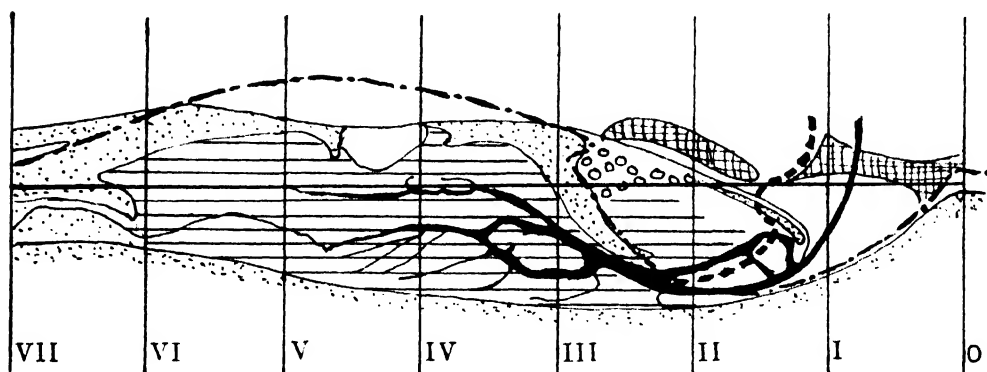
Fig. 1. Small scale map of the Marsh in 1931.

[▨▨] Vegetation of dunes and laterals.

o᳓o Embryonic dunes.

[≡] Vegetation of marsh.

━·━·━ Limits of vegetation in 1913.

[▦] Shingle banks in 1913.

■ ■ ■ ■ Course of east end of Channel in 1913.

The shore in VI–VII N on the other hand does not seem to be suffering erosion; where in 1913 there were embryo dunes there is now a definite ridge bearing a typical *Ammophila* vegetation.

At the west end of the marsh the increased number of bungalows has led to various minor changes, such as the widening of the cart-tracks and the removal of turf in places.

II. CHANGES IN THE VEGETATION.

The shingle bank at the mouth of the channel was described in 1928 (**3**) as having fused to the main dune ridge and as bearing a vegetation for the most part in the embryonic stage. The more eastern part has now almost reached the *Ammophila* dune condition. Behind it there has been considerable colonisation of the muddy sand. *Suaeda maritima* var. *macrocarpa* now forms

Phot. 1. Looking eastwards across the shingle fan in IV-V N. *Ammophila arenaria* and *Suaeda fruticosa* in the foreground. Expanse of sand in the centre, marsh vegetation on the right; on the left are the shore and sea.

Phot. 3. Looking eastwards from a point S. of post 11. showing colonisation of sandy mud by *Suaeda fruticosa* var. *macrocarpa*. The sandy tussocks on the right are

Phot. 2. Detail from Phot. 1 showing *Suaeda fruticosa* bushes with dying branches on the seaward side.

CONWAY - SALTMARSH AT HOLME-NEXT-THE-SEA

a uniform though not dense covering over quite a large area (see Pl. XIII, phot. 2). It is, however, an annual and possibly at its greatest development in August so that its part in permanent colonisation may be small. Observation over a longer period would decide this point.

The *Glyceria-Obione* society on sandy mud has extended eastwards and *Statice limonium* and *Aster tripolium* have followed in the lower-lying parts, while *Suaeda fruticosa* has spread considerably, especially on a slight ridge parallel to the river.

The vegetation of the "lateral" round about post III corresponds to the description given in 1928 (**3**). The old breaches represented by shingle-fans thrown over the marsh in III–IV N seem to have been obliterated by the formation of a dune ridge, but the region of the marsh just inside the dunes seems complex and further work on it is at present in progress.

Except near the mouth the limits of the main communities have changed little. The western end of the marsh has become drier if judged by a comparison of the number of pools but this does not necessarily indicate less frequent inundation by the tide.

The following notes deal with the distribution of particular species.

Suaeda fruticosa. The spread over the "new lateral" in II–III has been described (**2** and **3**). More bushes occur scattered along the edges of the channels than in 1913 and a most striking feature is the large number which occupy the banks of the main channel in V to VI S. In 1913 this was characterised by an abundance of *Suaeda maritima* var. *flexilis*, of which there are now few specimens in that region. Oliver and Salisbury (**4**) state the following points with regard to *Suaeda fruticosa*:

(1) It is a shingle plant.
(2) It flourishes in places where the tidal drift carries an abundance of seed.
(3) It needs a fairly stable substratum or the seedlings cannot survive.
(4) It may flourish better where there is some quantity of humus.

That it is not exclusively a shingle plant is proved by its distribution in this marsh, and it is noticeable that the bushes which grow in mud or sandy mud generally show a more luxuriant growth than those which grow on shingle. Conditions (2), (3) and (4) are fulfilled by the habitats in which the bush occurs here.

There has been a great loss of bushes from the distal end of the lateral in IV–V N. Further the line of bushes on the seaward border of the new shingle fan is looking very sickly, especially those branches on the seaward side (see Pl. XIII, phot. 2). A possible explanation is that damage is done by onshore winds which may be very fierce and carry much sand with them; if this is so it may be that the death of the bushes on the tip of the lateral is due to loss of the shelter originally provided by the dune ridge which is now almost washed away. Shelter from wind and the frequently accom-

panying sand may, therefore, be another factor limiting the distribution of this species.

Obione portulacoides. Since 1913 the fringes along the main channels have extended along the smaller tributaries, often nearly blocking them, but the most striking spread has occurred in the region between III and IV where it now dominates definite areas forming a well-marked society. Occasional tufts of *Glyceria maritima* are found in this society, but they look unhealthy and are rare where the *Obione* is most luxuriant. This society may be described as:

Obione portulacoides	d.	Salicornia europaea	o.
Suaeda maritima var. flexilis	a.	Glyceria maritima	o.
Aster tripolium	l.a.		

The *Aster* is especially characteristic of the channels which are being blocked up.

The belts of *Obione* just inside the *Suaeda fruticosa* zone are not so well-marked as in 1913, but the distribution in the western *Armeria* zone and in the shingle patches corresponds closely to the description given then (1). The factors which govern the distribution of *Obione* are at present rather obscure. It has the most luxuriant vegetative growth in the mud of the central regions of the marsh but though its size is less on sand or shingle it seems to thrive satisfactorily. A possible explanation is that it cannot stand waterlogged soil for long periods. This is supported by the recent observations of a party from the Cambridge Botany School that it does not grow on soil lower than a certain level, and by its position on channel banks where the soil would remain waterlogged for a minimal length of time.

Aster tripolium. On the south of the main channel this species only occurred occasionally further east than about halfway between III and IV, whereas in the 1913 map it is indicated as occurring abundantly well in the *Glyceria-Salicornia* region of II–III S, i.e. the species seems to have retreated to the west. This plant very often seems to be the second species to colonise bare mud. It may be seen associated with *Glyceria* or *Salicornia* in drying pools or on islands in the channel, but is rarely seen by itself in such a position. Possibly the seedlings are easily washed out of bare mud, but at present the distribution of the species has no obvious explanation.

GENERAL DISCUSSION.

The factors mainly responsible for the distribution of the salt-marsh societies are difficult to distinguish clearly and much work remains to be done on water levels, drainage, aeration of the soil, nature and effect of the deeper-lying soils, and so on.

That *Armeria* needs a definitely sandy soil to become dominant seems established by the diggings and soil analyses made by Marsh in 1913 (1). The central position of the *Statice* society, coinciding roughly with the area

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covered by the ordinary spring tides, suggests that the conditions favouring it are either a larger proportion of mud in the soil or more frequent inundation by sea water than occurs in the *Armeria* zone. But more frequent inundation would also involve the greater deposition of mud, so that the two effects can only be separated by experiment. One of the most difficult regions of vegetation to interpret is the zone of *Armeria* surrounding the tip of the lateral in IV–V N. This is low-lying and seems to be no different from other regions where *Statice limonium* is present, but sand blown in from the dunes may be an important factor in this region.

With regard to the succession of the societies it seems likely that the scheme given by Marsh (1) may need certain alterations in detail, for example, the *Statice* society may possibly follow "*Glyceria-Obione* on sand." The presence of a definite *Obione* society is a further complication and the extent to which it will spread and how far it will affect the general succession is difficult to predict without further knowledge.

Marsh suggested that the *Armeria* zone was extending eastwards so as to replace the *Statice* society, but the process does not seem to have gone far since then, judging by the two maps. It is possible that the succession over the marsh in general has not advanced as might have been expected, because the erosion of the shore has allowed the tide to enter more freely so that the raising of the soil-level by the deposited mud and by sand blown in from the dunes has been balanced by the greater depth of immersion by the tide.

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SECOND REPORT ON THE TRANSPLANT EXPERIMENTS OF THE BRITISH ECOLOGICAL SOCIETY AT POTTERNE, WILTS.

By ERIC M. MARSDEN-JONES AND W. B. TURRILL.

(With Plates XIV and XV and four Graphs in the Text.)

SINCE the preparation of the first report (October, 1929) the Transplant Committee has met at Potterne and Kew and has approved the methods of conducting the experiments in 1930 and 1931. At the last meeting the Committee decided to discontinue the experiments with *Silene vulgaris* and to reduce the number of *Anthyllis* plants. It was also decided to accept Dr Gregor's offer of cloned diploids and hexaploids of *Phleum pratense* for transplantation.

The material of *Fragaria vesca* was cloned and transplanted in the spring of 1932.

The Committee suggested that preliminary experiments should be made with *Ononis spinosa* L. and its var. *mitis* (L.), *Solanum dulcamara* L. var. *marinum* Bab. and *Bellis perennis* L.

Only a few references are made in this report to the reserve plants at Kew, because in the middle of the period they had to be moved to a new Herbarium Ground owing to building operations.

Corrections. The position of Potterne (first report, this JOURN. **18**, 352) should read lat. 51° 21' N. and long. 2° W. The K_2O (total) for calcareous sand (*l.c.* p. 354) should read 0·1581 not 0·1548.

METEOROLOGICAL DATA.

1930	Temperature Max. °C.	Max. °F.	Min. °C.	Min. °F.	Relative humidity Max. %	Min. %	Rainfall in mm. Week	Month	No. of "rain days" Week	Month
Jan. 1– 7	10·6	51	– 1·1	30	95	57	23·7		4	
,, 8–14	12·2	54	– 1·1	30	95	60	30·0		4	
,, 15–21	15·0	59	0	32	95	58	0·0		0	
,, 22–28	8·9	48	– 0·6	31	93	59	30·2		6	
,, 29–31	8·9	48	– 1·1	30	93	53	16·0	99·9	2	16
Feb. 1– 7	7·2	45	– 1·1	30	95	58	8·2		3	
,, 8–14	7·8	46	– 2·2	28	95	54	1·5		1	
,, 15–21	7·8	46	– 3·9	25	95	45	0·5		1	
,, 22–28	11·1	52	– 2·8	27	93	59	2·5	12·7	2	7
Mar. 1– 7	13·3	56	– 0·6	31	95	56	6·7		3	
,, 8–14	11·1	52	– 0·6	31	95	42	20·2		6	
,, 15–21	11·1	52	– 11·7	11	95	51	14·0		2	
,, 22–28	17·2	63	– 1·1	30	95	43	3·5		3	
,, 29–31	18·3	65	1·1	34	94	50	3·0	47·4	1	15

Phot. 1. *Right-hand row*: "calcareous sand" in front, "chalky clay" behind. *Left-hand row*: "sand" in front, "clay" behind. Reserves on Potterne soil to left of left-hand row. Each enclosure except the Potterne soil is 35 × 10 × 3 feet and contains about 50 tons of soil. Meteorological instruments between the rows.

Phot. G. Atkinson, 7. vii. 1930.

MARSDEN-JONES AND TURRILL—REPORT ON TRANSPLANT EXPERIMENTS
AT POTTERNE

1930	Temperature Max. °C.	Max. °F.	Min. °C.	Min. °F.	Relative humidity Max. %	Min. %	Rainfall in mm. Week	Month	No. of "rain days" Week	Month
Apr. 1– 7	17·8	64	1·1	34	95	47	19·5		3	
„ 8–14	20·6	69	0	32	95	43	14·5		5	
„ 15–21	13·3	56	0	32	95	48	8·7		3	
„ 22–28	19·4	67	3·9	39	94	44	15·2		3	
„ 29–30	20·0	68	0·6	33	95	38	0·0	57·9	0	14
May 1– 7	20·6	69	2·8	37	95	39	21·7		4	
„ 8–14	18·9	66	3·3	38	95	48	13·7		4	
„ 15–21	20·6	69	4·4	40	95	45	1·5		2	
„ 22–28	24·4	76	6·7	44	95	40	5·0		3	
„ 29–31	23·9	75	10·6	51	94	42	7·5	49·4	3	16
June 1– 7	32·8	91	6·1	43	94	32	0·2		1	
„ 8–14	30·6	87	6·7	44	95	40	16·0		1	
„ 15–21	28·3	83	10·0	50	94	42	1·5		1	
„ 22–28	26·7	80	5·0	41	94	36	4·0		2	
„ 29–30	30·0	86	12·8	55	94	36	11·5	33·2	1	6
July 1– 7	30·0	86	8·9	48	94	35	0·0		0	
„ 8–14	26·7	80	6·7	44	94	34	4·7		2	
„ 15–21	20·6	69	6·1	43	92	44	23·2		6	
„ 22–28	21·1	70	8·9	48	93	52	13·2		6	
„ 29–31	23·3	74	7·8	46	93	42	13·0	54·1	2	16
Aug. 1– 7	22·2	72	7·2	45	94	46	41·0		4	
„ 8–14	24·4	76	11·1	52	91	46	5·0		3	
„ 15–21	22·2	72	6·1	43	94	46	22·0		5	
„ 22–28	34·4	94	8·3	47	90	46	5·7		3	
„ 29–31	34·4	94	8·3	47	93	40	0·0	73·7	0	15
Sept. 1– 7	28·3	83	6·7	44	93	38	1·2		2	
„ 8–14	22·2	72	5·6	42	92	52	18·2		4	
„ 15–21	20·0	68	7·8	46	94	55	49·5		7	
„ 22–28	24·4	76	6·1	43	93	52	9·2		6	
„ 29–30	19·4	67	7·8	46	92	57	5·7	83·8	1	20
Oct. 1– 7	19·4	67	7·2	45	92	56	13·0		5	
„ 8–14	18·3	65	0·6	33	92	49	6·0		2	
„ 15–21	18·9	66	2·8	37	93	52	11·5		5	
„ 22–28	13·3	56	0	32	93	57	10·5		5	
„ 29–31	14·4	58	8·3	47	92	63	5·2	46·2	2	19
Nov. 1– 7	13·9	57	−3·9	25	93	46	15·2		3	
„ 8–14	15·6	60	−2·2	28	93	50	0·0		0	
„ 15–21	13·3	56	−8·3	17	92	56	41·5		5	
„ 22–28	13·3	56	−1·1	30	93	54	44·7		7	
„ 29–30	7·8	46	5·6	42	90	82	1·2	102·6	1	16
Dec. 1– 7	8·9	48	−1·7	29	92	75	12·5		2	
„ 8–14	10·0	50	−5·0	23	91	65	24·5		5	
„ 15–21	8·9	48	−2·8	27	92	64	11·0		2	
„ 22–28	11·1	52	−1·1	30	90	67	15·7		4	
„ 29–31	8·9	48	−2·2	28	92	72	16·5	80·2	3	16
1931										
Jan. 1– 7	4·4	40	−7·2	19	91	75	3·7		2	
„ 8–14	6·7	44	−7·2	19	90	54	3·0		2	
„ 15–21	10·6	51	−0·6	31	93	56	3·5		4	
„ 22–28	9·4	49	−2·8	27	94	56	25·0		6	
„ 29–31	6·7	44	−2·8	27	93	64	12·7	47·9	2	16
Feb. 1– 7	8·3	47	−3·3	26	93	58	8·2		4	
„ 8–14	11·1	52	−3·3	26	94	48	20·7		6	
„ 15–21	9·4	49	−2·2	28	94	53	16·7		6	
„ 22–28	11·1	52	−1·1	30	94	48	15·7	61·3	4	20
Mar. 1– 7	8·3	47	−5·6	22	90	38	5·0		2	
„ 8–14	12·8	55	−11·1	12	92	40	1·5		1	
„ 15–21	16·7	62	−2·8	27	92	40	5·0		1	
„ 22–28	20·6	69	−2·2	28	93	32	0·5		1	
„ 29–31	12·2	54	2·2	36	75	35	0·5	12·5	1	7

1931	Temperature Max. °C.	Max. °F.	Min. °C.	Min. °F.	Relative humidity Max. %	Min. %	Rainfall in mm. Week	Month	No. of "rain days" Week	Month
Apr. 1– 7	20·6	69	0·6	33	90	35	28·7		5	
„ 8–14	20·6	69	1·1	34	93	37	3·2		1	
„ 15–21	15·0	59	0	32	94	39	13·2		5	
„ 22–28	14·4	58	0	32	93	47	24·0		6	
„ 29–30	17·8	64	0	32	90	41	0·0	69·1	0	17
May 1– 7	20·0	68	0	32	93	37	8·7		3	
„ 8–14	23·3	74	5·6	42	93	32	8·0		2	
„ 15–21	17·8	64	1·1	34	92	44	9·2		4	
„ 22–28	24·4	76	6·7	44	92	42	35·0		4	
„ 29–31	20·0	68	8·9	48	92	51	2·5	63·4	3	16
June 1– 7	28·9	84	6·7	44	91	41	13·5		4	
„ 8–14	23·3	74	10·0	50	93	50	36·0		5	
„ 15–21	23·3	74	7·8	46	92	44	15·2		3	
„ 22–28	26·1	79	3·3	38	93	41	7·0		1	
„ 29–30	27·8	82	7·8	46	91	36	0·0	71·7	0	13
July 1– 7	26·7	80	7·2	45	92	47	25·5		6	
„ 8–14	23·3	74	7·8	46	93	50	41·0		6	
„ 15–21	21·1	70	4·4	40	92	47	15·0		5	
„ 22–28	25·0	77	8·9	48	90	43	24·5		4	
„ 29–31	23·3	74	11·1	52	90	52	1·7	107·7	1	22
Aug. 1– 7	26·7	80	10·6	51	91	46	10·0		3	
„ 8–14	23·3	74	6·1	43	93	33	24·5		4	
„ 15–21	22·8	73	6·7	44	92	47	41·2		5	
„ 22–28	25·6	78	3·3	38	93	36	5·5		1	
„ 29–31	22·8	73	9·4	49	90	50	5·7	86·9	2	15
Sept. 1– 7	20·0	68	1·7	35	92	47	44·7		6	
„ 8–14	20·6	69	1·7	35	90	40	1·5		2	
„ 15–21	23·3	74	3·3	38	92	42	2·2		1	
„ 22–28	16·7	62	3·3	38	90	42	0·0		0	
„ 29–30	16·7	62	8·9	48	86	51	0·0	48·4	0	9
Oct. 1– 7	20·0	68	5·6	42	90	45	24·5		3	
„ 8–14	21·1	70	1·1	34	90	40	2·0		2	
„ 15–21	17·2	63	−4·4	24	92	48	0·0		0	
„ 22–28	13·3	56	−5·6	22	93	44	0·0		0	
„ 29–31	11·1	52	−1·7	29	90	54	1·0	27·5	1	6
Nov. 1– 7	20·0	68	4·4	40	92	41	45·7		5	
„ 8–14	13·3	56	1·1	34	92	51	17·2		5	
„ 15–21	11·1	52	0	32	92	56	9·2		3	
„ 22–28	12·2	54	0·6	33	90	56	16·2		5	
„ 29–30	5·6	42	3·3	38	87	80	2·0	90·3	1	19
Dec. 1– 7	13·9	57	−1·7	29	90	56	15·7		5	
„ 8–14	11·1	52	1·7	35	90	71	0·0		0	
„ 15–21	8·9	48	−6·7	20	88	64	1·7		1	
„ 22–28	11·1	52	−1·7	29	88	57	2·0		2	
„ 29–31	6·7	44	−6·7	20	90	56	2·5	21·9	1	9

RAINFALL. 1929.

November	mm.	December	mm.
1– 7	18·0	1– 7	52·5
8–14	19·5	8–14	40·5
15–21	35·5	15–21	14·0
22–28	61·7	22–28	17·5
29–30	7·5	29–31	7·5
Totals	142·2		132·0

The rainfall figures for November and December, 1929, are given in order to complete the records since the meteorological instruments were installed

(see first report, p. 355). For 1930 the total annual rainfall was 761·1 mm. (30·8 in.) and for 1931 708·6 mm. (28·4 in.). The absence of any long dry summer period characterised both years, especially the latter. The effects of prolonged summer drought recorded for 1929 in the first report were not therefore repeated. The distribution of rainfall throughout the warmer months of the year and the consequent usually high soil moisture content affected the plants by "puddling" of the clays and by affording favourable conditions for slug development. It also favoured the development of mosses and the increase of snails (see below).

ADVENT OF BIOTIC FACTORS.

In the winter of 1929–30 mosses appeared in some abundance on the undisturbed parts of the beds not occupied or shaded by the plants. In order of greatest area covered by moss (regardless of the species) the beds were scored on 27. i. 30: calcareous sand, chalky clay, sand, Potterne soil, clay. This order was retained throughout the period under review in this paper, i.e. up to December, 1931. The species recorded were:

Sand:

Bryum sp. (barren) 1930, 1931.   Brachythecium glareosum B. et S. 1931.
Hypnum sp. (barren) 1930.   Bryum atropurpureum W. et M. (probably) 1931.
Ceratodon purpureus Brid. 1931.   Pottia truncatula Lindb. 1931.

Calcareous sand:

Bryum argenteum L. 1930, 1931.   Funaria hygrometrica Sibth. 1931.
Barbula unguiculata Hedw. 1930, 1931—
    abundant.

Clay:

Barbula unguiculata Hedw. 1931.

Chalky clay:

Pottia truncatula Lindb. 1930.   Brachythecium glareosum B. et S. 1931.
Barbula convoluta Hedw. 1930.   Barbula unguiculata Hedw. 1931.
Phascum cuspidatum Schreb. 1930.   Funaria hygrometrica Sibth. (a very little) 1931.

Reserves on Potterne soil:

Bryum sp. (barren) 1931.   Pottia truncatula Lindb. 1931.
Phascum cuspidatum Schreb. 1930, 1931.   Barbula convoluta Hedw. 1931.
Eurhynchium praelongum Hobk. 1931.   Ceratodon purpureus Brid. 1931.

By far the most abundant were the species of *Barbula*, especially on the calcareous soils. On the calcareous sand the mosses threatened to compete with the transplants and the surface had to be forked over. Successional studies of an immigrant flora are beyond the scope of the experiments and would interfere with their main purposes. A species of *Cladonia* (barren) appeared on the sand in the autumn of 1931 in two small patches. For the mosses the species standard and nomenclature follow Dixon: *Student's Handbook of British Mosses*, ed. 3, 1924. Specimens are preserved in the Herbarium of the Royal Botanic Gardens, Kew.

A second biotic factor was slugs. Slug attack was first noted on June 22nd,

1931. The pest increased greatly and rapidly on the clay and chalky clay. The principal damage has so far been done to *Silene maritima* on the clays. The eating off of the hemicryptophytic shoots and the crown has been the cause (or at least one main cause) of very many deaths. On December 31st, 1931, a few slugs were found round *Silene maritima* plants on the sands. On the same date it was recorded that slugs had damaged the *Centaurea* plants, but only on the clay, where the basal winter-green leaves were mostly eaten to the midrib[1].

Perhaps under the heading of biotic factors the influence of own top-hamper should be mentioned. "Smothering by own top-hamper" is a phrase which at least describes what appears to be the cause of death or of much reduced vitality in some of the plants. It was especially recorded for the inner rows of *Centaurea*. The dense dead mass of stems and leaves reduced the amount of light reaching the winter-green basal leaves and young spring shoots. Products of decay may have a toxic effect. Sometimes, however, the action is more indirect. A contributory cause of death of *Silene maritima* plants on the clays was that the top-hamper led to the compacting (water-logging and surface hardening) of the soil around the plants by retarding the entrance of frost and the evaporation of water. Experience with the trans-plants has shown how well justified is the gardening practice of clearing away organic débris and of periodically moving or repropagating herbaceous perennials of many kinds.

Centaurea nemoralis Jord. forma radiata albiflora

Winter condition and deaths. On the whole *Centaurea* is the most persistent (i.e. the best) perennial of the species at present in position on the various soils. Deaths occurred as follows: spring 1930 ($2\frac{1}{2}$ years from cloning), on clay 2, reserve 5, the latter only were replaced by new clones; spring 1931, no further deaths; autumn 1931 (4 years from cloning), one on chalky clay.

The tufted nature of growth, and the production of large numbers of leafy flowering stems results in the formation of an abundance of "top-hamper"

[1] Slugs and snails on transplant soils, collected May, 1932:

Sand: *Agriolimax agrestis*, 2.

Calcareous sand: *Agriolimax agrestis*, 10.

Clay: *Arion hortensis*, 14; *Hyalinia cellaria*, 2 (snail).

Chalky clay: *Agriolimax agrestis*, 6; *Hyalinia cellaria*, 6.

Potterne soil: *Agriolimax agrestis*, 6 (one black, rather rare); *Arion hortensis*, 4.

Prof. Boycott, President of the British Ecological Society, who has very kindly named the above recorded material, writes: "it is rather curious that *Arion hortensis* is found only on two of the five plots: it is in general about the most abundant garden slug we have." The figures given after each species represent the number of specimens collected and sent to Prof. Boycott. No attempt was made at this time to estimate the slug and snail populations of the plots. The occurrence of one species in such abundance as to be an important (if not the chief cause) of the destruction of most plants of *Silene maritima* on the calcareous sand was recorded for the date 8. v. 32. The sand was then still relatively free from Mollusca.

in the autumn. This gradually decays and breaks down, the foliage first and the stems more gradually—often remaining for two years. The breaking down and decay was quickest on clay and slowest on calcareous sand in both seasons.

Seedlings.

	Spring, 1930	Autumn, 1930	Spring, 1931
Sand	Numerous	Few	Numerous
Calcareous sand	Numerous	Few	Numerous
Clay	About 3	None	None
Chalky clay	Numerous	Few	Very few
Potterne soil	About 12	Very few	Few

The statement made in the first report (p. 359) that the main germination is in the spring, but that there is a certain amount of continuous germination throughout the year has been substantiated. In the summer and autumn of 1931 the total top-hamper of the several years had become so dense that it was impossible for many seedlings to germinate and fewer still to survive.

General tone. In 1930 the tone was equally good on all soils. In the summer of 1931 it gradually became best on calcareous sand and worst on clay, but in December the winter condition was best on sand. The plants in the outside rows on all the soils were much more vigorous than those in the centre. The marked effect of smother is emphasised by the much reduced size and vigour of most of the plants in the central rows, especially on the clays, and the fact that the only deaths to date have been in these central rows.

Habit and stem heights. The marked differences in habit between the plants at Potterne and at Kew (see first report, p. 358) have been maintained. On all the soils the plants are now showing centrifugal spread with a tendency to form hollow centres. This is comparable to observations we have made in nature.

Stem heights (maximum for each soil).

	7. vii. 30	18. viii. 31
	dm.	dm.
Sand	10	9·2
Calcareous sand	10	10·2
Clay	8·5	8
Chalky clay	10·7	8·7
Potterne soil	7·5	8·5

Numbers of flowering stems per plant.

	Sand		Calcareous sand		Clay		Chalky clay		Potterne soil	
	1930	1931	1930	1931	1930	1931	1930	1931	1930	1931
Maximum	62	40	84	85	64	66	82	105	45	56
Minimum	20	8	13	8	15	2	17	2	3	12
Mean	38·3	25·7	42·4	38·2	42·3	30·3	52·8	41·1	23·2	39·0
Standard deviation	12·5	9·9	17·3	21·3	14·8	20·8	10·2	24·6	11·7	17·2

In preparing the above table dead plants (two in clay for 1930 and 1931) have been omitted entirely. A discussion of the figures is reserved till counts are available for a longer series of years.

Indumentum. The original cloned parent had short scattered pubescence on both surfaces of the basal leaves. This condition was maintained in 1930 and 1931 in the plants on clay and Potterne soil. The plants on sand, calcareous

sand, and calcareous clay appeared slightly lighter green in colour, and on examination the hairs were found to be somewhat shorter and less numerous.

Primary flowering. In 1930 and 1931 it was impossible to record the appearance of first flowers on individual plants because of the dense interlacing growth. The occurrence of the first flowers on each of the soils was, however, recorded. The following sequences were thus obtained for both 1930 and 1931: calcareous sand, sand, Potterne soil, chalky clay, clay.

Completion of primary flowering (recorded July 21st, 1930 and July 20th, 1931). The sequence in each year was: sand (completed first), calcareous sand, chalky clay, Potterne soil, clay.

Secondary flowering occurred in 1931 on many plants with the following order for the different soils: Potterne soil (most capitula), clay, calcareous clay, calcareous sand, sand. The flowering on all soils was completed by August 14th.

Silene vulgaris Garcke.

Winter condition and deaths. The species is a typical hemicryptophyte. After fruiting, usually in July, the aerial parts die down, some secondary shooting occurring on old branches and from the crown. The real overwintering buds are generally just above ground by mid-winter, those of the transplant stock showing much anthocyanin.

Winter deaths 1929–30 ($1\frac{1}{2}$–2 years old): sand Nos. 1, 6, 7, 19, 25 a; Potterne soil Nos. 134, 148.

Summer deaths 1930 ($2\frac{1}{4}$ years old): sand No. 4.

Winter deaths 1931 (3 years old): sand Nos. 9, 13, 16; Potterne soil Nos. 128, 131, 136, 138, 141, 147.

Summer and autumn deaths 1931 ($3\frac{1}{2}$ years old): clay Nos. 51, 53, 54, 56, 57, 59, 60, 61, 62, 63, 65, 68, 69, 75; chalky clay Nos. 76, 78, 79, 81, 83, 84, 88, 89, 91, 92, 94, 95, 100; Potterne soil Nos. 129, 135, 139, 140, 143.

The lack of a dry summer spell and consequent rotting of the crowns together with bad slug attack probably caused the large number of deaths on the clays.

Disease. Marssonina attacked the plants on all the soils. The race is a very susceptible one and the degree of susceptibility is not affected by edaphic factors. The disease does not by itself cause the death of plants. The much greater resistance shown by *S. maritima* was marked on all the soils.

Seedlings. Two more years' experience confirms the natural spring germination of pure *S. vulgaris* seed.

Spring seedlings.

	11. v. 30	22. vi. 31
Sand	None	Few
Calcareous sand	Few	Few
Clay	Very few	Few
Chalky clay	Numerous	Few
Potterne soil	Very few	None

General tone. This showed much fluctuation, due to *Marssonina* and slug attack as well as to weather conditions. Placing the best tone first the sequences were:

16. iv. 30	23. vi. 30	15. iv. 31	16. v. 31	22. vi. 31
Sand	Chalky clay	Chalky clay	Chalky clay	Chalky clay
Calcareous sand	Clay	Calcareous sand	Calcareous sand	Clay
Clay	Potterne soil	Clay	Clay	Calcareous sand
Chalky clay	Calcareous sand	Sand	Potterne soil	Potterne soil
Potterne soil	Sand	Potterne soil	Sand	Sand

PRIMARY FLOWERING. PLANTS IN FLOWER, 1930.
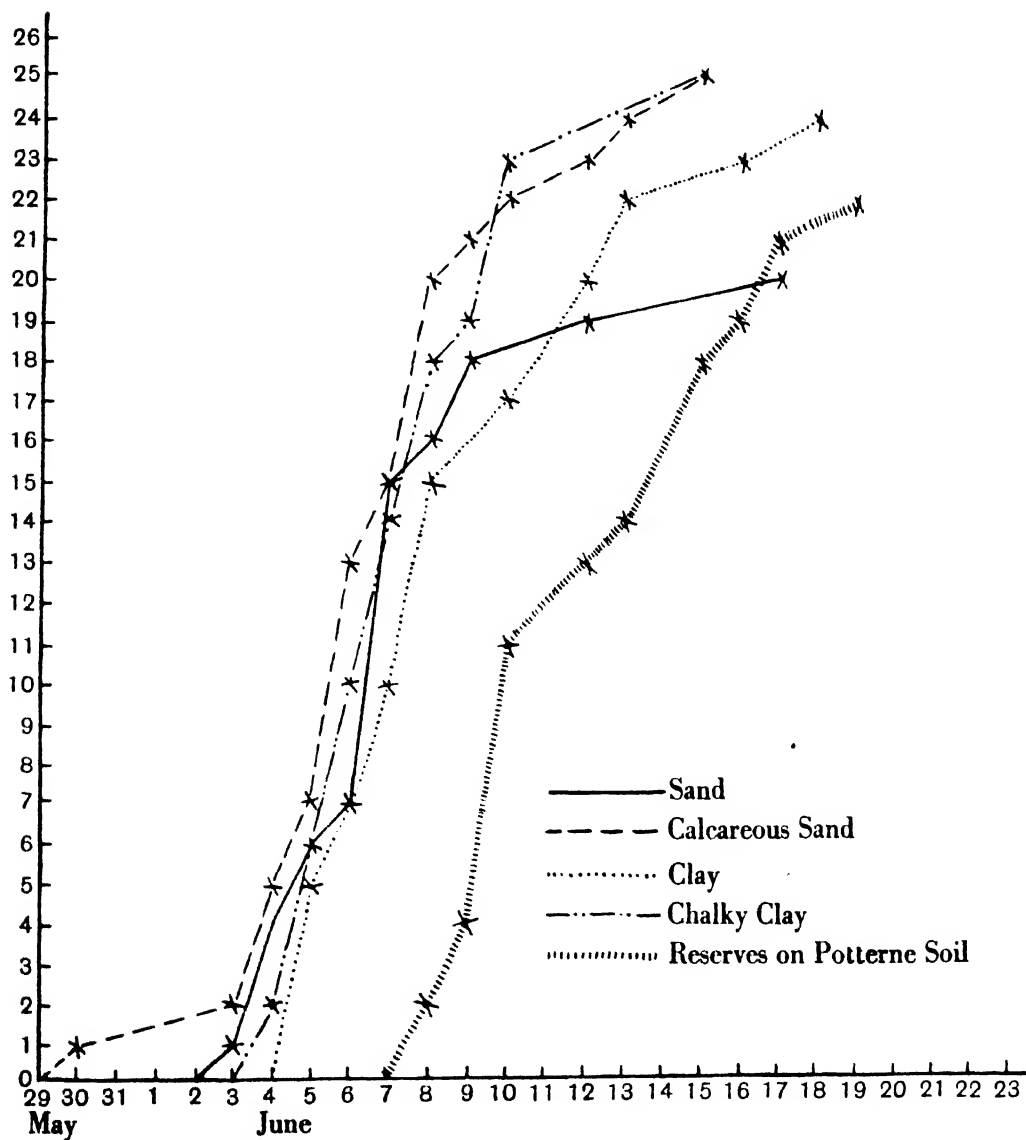
Fig. 1. *Silene vulgaris.* Graph showing numbers of plants in flower (ordinates plotted against dates (abscissae), 1930.

Habit. Sand, clay, chalky clay, and Potterne soil: no changes.

Calcareous sand: the strict habit became less marked in 1930 and much less in 1931. At the last recording only Nos. 31 and 48 retained some degree of strictness.

PRIMARY FLOWERING. PLANTS IN FLOWER, 1931.
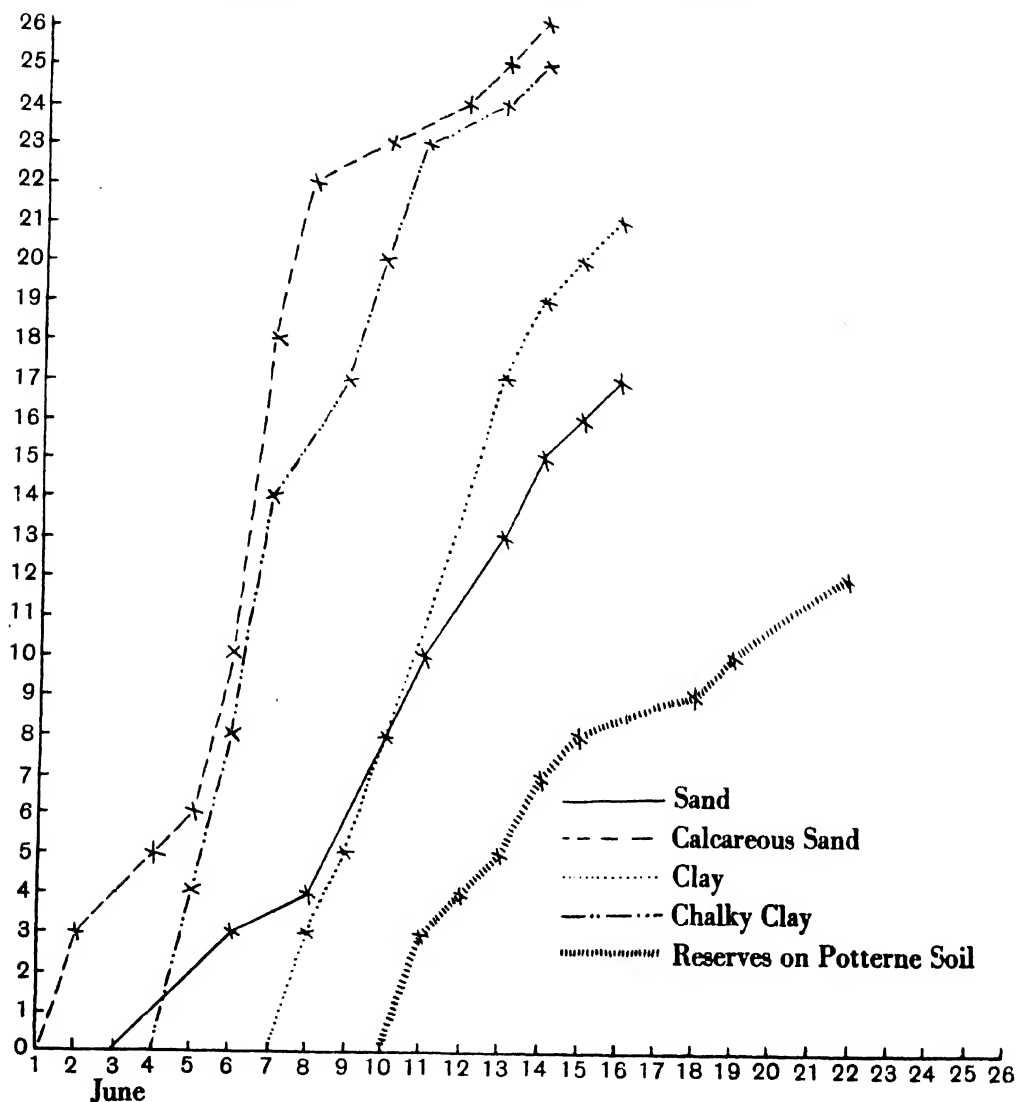
FIG. 2. *Silene vulgaris.* Graph showing numbers of plants in flower (ordinates) plotted against dates (abscissae), 1931.

Length of stems (measured on June 22nd, 1931).

Sand: max. (No. 18) 6 dm.; min. (No. 22) 1·8 dm.

Calcareous sand: max. (No. 42) 5·3 dm.; min. (No. 39) 1·8 dm.

Clay: max. (No. 70) 6·5 dm.; min. (No. 74) 2·4 dm.

Chalky clay: max. (No. 94) 5·5 dm.; min. (No. 84) 1·1 dm.

Potterne soil: max. (No. 146) 4·7 dm.; min. (No. 139) 1·4 dm.

Primary flowering and florifery. The graphs should be compared with that on p. 363 of the first report (this JOURN. **18**). It will be noted that the slower flowering of plants on Potterne soil has remained a constant feature for three years. With increasing age of the plants the relative precocity of flowering on calcareous sand has become more marked.

Florifery on the different soils was, in the order of greatest first: 1930, clay, chalky clay, Potterne soil, sand, calcareous sand; 1931, chalky clay, clay, calcareous sand, Potterne soil, sand.

Completion of primary flowering. On June 7th, 1930 and June 6th, 1931 primary flowering was completed on all soils.

Secondary growth.

Sand:	9. viii. 30	10. ix. 30	6. vii. 31
With green primary stems	1	0	0
Secondary growth from old stems	8	1	12
Secondary growth from crown	0	17	0
Secondary growth from old stems and crown	1	0	5
Calcareous sand:			
With green primary stems	7	0	0
Secondary growth from old stems	10	0	13
Secondary growth from crown	1	20	3
Secondary growth from old stems and crown	3	0	0
Clay:			
With green primary stems	1	0	0
Secondary growth from old stems	7	0	24
Secondary growth from crown	4	22	0
Secondary growth from old stems and crown	0	0	1
Chalky clay:			
With green primary stems	0	0	0
Secondary growth from old stems	5	0	23
Secondary growth from crown	8	23	1
Secondary growth from old stems and crown	2	0	1
Potterne soil:			
With green primary stems	2	0	0
Secondary growth from old stems	2	0	0
Secondary growth from crown	9	24	0
Secondary growth from old stems and crown	13	0	17

Secondary flowering.

	10. ix. 30	20. vii. 31 (buds only)
Sand	0	17
Calcareous sand	0	15
Clay	2	25
Chalky clay	6	14
Potterne soil	4	16

Colour of foliage. The plants on the clay retained and even intensified the light yellow-green colour noted in the first report (p. 363). On all the other soils the foliage colour was as in the original parent. No. 83, on calcareous clay, was found (September 29th, 1930) to have produced one variegated shoot whose leaves had cream-coloured margins tinged with purple antho-cyanin. The variegation was not reproduced in 1931.

Sex. This has been recorded for all first flowers. A practically complete morphological series from purely female flowers to those with a full comple-

ment of viable stamens was recorded. A full discussion of sex in *Silene* is reserved for a later paper.

ROOT SYSTEM. The committee having decided to discontinue the experiments with *Silene vulgaris* the first opportunity occurred of examining root systems of the transplants. The plants in any one soil showed marked uniformity of root systems. The following records were taken (31. xii. 31):

Sand. About five main roots branched 8–10 cm. below the crown and then ran straight down, without forking, to a depth of 6–7 dm. A few tuberous thickenings were present. The superficial colour of the washed roots was "Clay Color" (Ridgeway, Pl. XXIX).

Calcareous sand. About seven main roots, with little or no branching, ran straight down to a depth of 6–7 dm. Tuberous thickenings were not present. The superficial colour of the washed roots was "Antimony Yellow" (Ridgeway, Pl. XV).

Clay. About twelve main roots, three or four of which ran straight down but had decayed at 20–25 cm. depth. The remainder spread horizontally 4–5 cm. below the surface of the soil and to a distance of 6–7 dm. or more from the crown. A good deal of branching occurred at various distances from the crown. The superficial colour of the washed roots was "Chamois" (Ridgeway, Pl. XXX).

Calcareous clay. About twenty-four main roots, with little or no branching, ran straight down to a depth of 7 dm. The superficial colour of the washed roots was "Cream Buff" (Ridgeway, Pl. XXX).

Potterne soil. About four main roots were very much branched 5–8 cm. below the crown into approximately thirty branches. These were at first coiled into a bunch and then ran approximately straight down. A few tuberous or nodular thickenings occurred. The superficial colour of the washed roots was "Antique Brown" (Ridgeway, Pl. III).

Silene maritima L.

Winter condition and deaths. The species behaves as a combination of hemicryptophyte and chamaephyte. The number of aerial shoots remaining alive and retaining terminal buds varying especially with winter weather conditions.

	Winter, 1929–30	Winter, 1930–31
Sand	Much dying back	Little dying back
Calcareous sand	No dying back	Little dying back
Clay	Some dying back	Some dying back
Chalky clay	Much dying back	Much dying back
Reserve	Much dying back	Much dying back

On clay and chalky clay plants at the edges of the enclosures had their overhanging shoots markedly green and chamaephytic.

Winter deaths 1929–30 ($1\frac{1}{2}$–2 years old): sand Nos. 1, 2, 6, 7, 11, 12, 14, 15, 16, 17, 18, 19 (these deaths were really due to the drought of September,

1929); clay No. 74; Potterne soil Nos. 126, 132, 134, 142. All the plants on Potterne soil dead up to June, 1930 were replaced with seedlings from No. 130 protected and selfed.

Summer deaths 1930 ($2\frac{1}{2}$ years old): sand Nos. 5, 22, 23, 25 a; clay No. 70; Potterne soil (6 months old) Nos. 148, 149.

Winter deaths 1930–31 ($2\frac{1}{2}$–3 years old): clay Nos. 54, 56, 57, 61, 62, 63, 67, 68, 69, 71, 75, 75 a; chalky clay Nos. 78, 84, 90, 91, 97; Potterne soil (various ages) all dead. All the plants on sand dead up to April, 1931 were replaced with seedlings from No. 13 protected and selfed.

Summer and autumn deaths, 1931: sand (various ages) Nos. 7, 10, 14, 23; clay ($3\frac{1}{2}$ years old) Nos. 50, 51, 52, 55, 59, 60, 61, 62, 64, 65, 66, 72; chalky clay ($3\frac{1}{2}$ years old) Nos. 77, 79, 80, 81, 82, 83, 85, 86, 87, 88, 89, 92, 93, 94, 95, 96, 98, 99, 100, 100 a.

Cuttings have been taken from plants on clay and chalky clay and No. 53 on clay was protected, selfed, and seed obtained. Replacements were made in the next spring.

Seedlings.

	Autumn 27. i. 30	Spring 16. iv. 30	Spring 11. v. 30	Autumn 29. ix. 30
Sand	Very numerous	Very few	Few	Numerous
Calcareous sand	Very numerous	Numerous	Numerous	Very numerous
Clay	Rotted off	None	None	Very few
Chalky clay	Very numerous	Numerous	Very numerous	Very numerous
Potterne soil	Numerous	Very few	2	Very few

It was noted in January, 1930, that the seedlings had not been tested by severe frost, but that they tended, especially on clay, to rot off with the excessive damp.

	Autumn 19. i. 31	Spring 15. iv. 31	Spring 16. v. 31	Autumn 31. xii. 31
Sand	Few	Few	Few	Few
Calcareous sand	Numerous	Numerous	Numerous	Very few
Clay	None	Very few	None	None
Chalky clay	None	None	None	None
Potterne soil	None	None	None	None

Seedlings damped off very badly in the autumn of 1930, and slug attack in 1931 on the clays also reduced the seedlings.

General tone. Placing the best tone first the sequences were:

16. iv. 30	29. ix. 30	15. iv. 31	16. v. 31	20. ix. 31
Calcareous sand	Chalky clay	Calcareous sand	Calcareous sand	Calcareous sand
Chalky clay	Potterne soil	Sand	Sand	Sand
Clay	Calcareous sand	Chalky clay	Clay	Clay
Sand	Clay	Clay	Chalky clay	Chalky clay
Potterne soil	Sand	—	—	—

Habit. Rooting at the nodes of old prostrate stems which usually then rot off from the rootstock was first recorded in five plants on April 16th, 1930 on sand. Since that date it has been observed on all the plots except that of Potterne soil.

Changes in habit occurred as follows:

1930.

Sand. Nos. 3, 4, 8, 9, 10, 13, 20, 21, 24, 25 had small leaves and flat habit as in class A of first report, p. 368.

Calcareous sand. Nos. 45, 49 were conspicuous in being similar in the flat habit to the plants on the sand. The remainder also had leaves smaller than those of the original parent.

Clay. The recording for habit was the same as that in the first report, p. 368, except that Nos. 57, 62 and 72 constituted class A and 54 was placed in class B.

Chalky clay. Nearly uniform and as in parent.

Potterne soil. Uniform and as in parent.

1931.

Sand. Nos. 4, 8, 13, 25 were the largest plants and had slightly larger leaves than the remainder but the general level of change from the parental type was maintained.

Calcareous sand. Three classes were recognised at the recording at maximum development (22. vi. 31): A (smallest leaves, plants most adpressed) Nos. 31, 34, 36, 38, 45, 49; B (intermediate between A and C) Nos. 27, 37, 42, 43, 46, 48, 50, 50 a; C (relatively largest leaves, less adpressed) Nos. 26, 28, 29, 30, 32, 33, 35, 39, 40, 41, 44, 47.

Clay. All the plants alive had become woody. Prostrate stems radiated out from the centre and were bare of leaves for a considerable distance but produced densely tufted leaves and shoots near the ends. Thus No. 73 had stems 6 dm. long, with 4·3 dm. practically bare of leaves.

Chalky clay. The one plant left alive retained the parental habit.

Diameter of plants.

	7. vii. 30		22. vi. 31	
	Max.	Min.	Max.	Min.
Sand	6·5 dm. (No. 4)	1·2 dm. (No. 3)	6 dm. (No. 25)	1·7 dm. (No. 10)
Calcareous sand	8·3 dm. (No. 47)	2·5 dm. (No. 45)	8 dm. (No. 44)	3·4 dm. (No 45)
Clay	10·5 dm. (No. 64)	5·2 dm. (No. 62)	—	—
Chalky clay	10·2 dm. (No. 76)	6·9 dm. (No. 98)	—	—
Potterne soil	8·7 dm. (No. 130)	6 dm. (No. 127)	—	—

Primary flowering and florifery. The former is given in graph form for 1930 only because of the large number of deaths on some of the soils (as given above). The most marked feature is the greatly extended period of time over which the plants showed first flowers, though this is much less marked on the calcareous soils. Comparison should be made with the graph of the first report, p. 366.

Florifery on the different soils was, in order of greatest first: 1930, chalky clay, calcareous sand, clay, Potterne soil, sand; 1931, calcareous sand, sand, (clay), (chalky clay).

Completion of flowering. The soil on which primary flowering was first completed placed first:

1930	1931
Calcareous sand	Calcareous sand
Clay	Sand
Chalky clay	Chalky clay
Potterne soil	Clay
Sand	—

PRIMARY FLOWERING. PLANTS IN FLOWER, 1930.
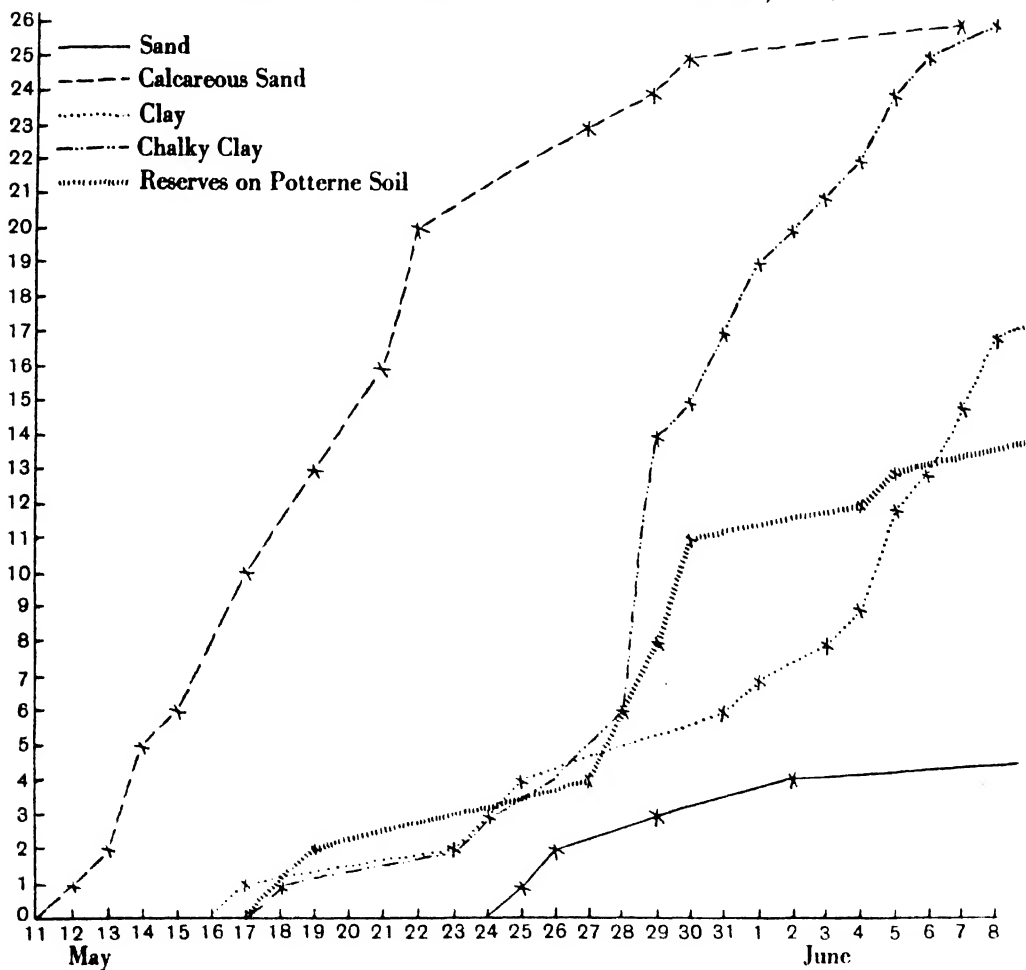
FIG. 3. *Silene maritima.* Graph showing numbers of plants in flower (ordinates) plotted against dates (abscissae). Additional dates, not shown on the graph, are:

Sand: July 11th, 5; July 15th, 6; July 20th, 7.

Clay: June 12th, 18; June 15th, 20; June 25th, 21; June 26th, 22; July 4th, 23.

Reserves on Potterne soil: June 13th, 15; June 15th, 16; June 17th, 17; July 2nd, 18; July 6th, 19.

In 1931 on the clays primary and secondary flowering were scarcely distinguishable.

Secondary flowering. In 1930 this was very pronounced.

Sand: 4 plants in flower, very few flowers per plant.

Calcareous sand: 20 plants in flower, few flowers per plant.

Clay: 14 plants in flower, very few flowers per plant.

Chalky clay: all plants in flower, few to many flowers per plant.

Potterne soil: all plants, except 150 *a*, in flower, very few flowers per plant.

Secondary flowering in 1931 was marked on sand and calcareous sand. The few plants which did not die on the clays flowered very late and sparsely.

Colour of foliage.

Sand: darker green than original and with more anthocyanin.

Calcareous sand: considerable range, Nos. 26, 44, 46 lighter than parent, Nos. 45, 49 were darker than parent, others approximately as parent. The actual shade, however, fluctuates from one group to another between recordings.

Clay: plants on the whole lighter (yellower) green than parent.

Chalky clay: plants on the whole darker (more blue) green than parent.

Potterne soil: uniform as original parent.

Calyx shape.

Sand: as original parent.

Calcareous sand: in 1930 the calyces were narrower than in parent, No. 48 becoming almost cylindric; in 1931 the narrowness was scarcely evident except that No. 48 still retained its almost cylindric shape.

Clays: for 1930 and 1931, calyces somewhat broader and more inflated than in parent.

Potterne soil: as original parent.

Calyx colour. The plants on the calcareous sand showed more reddish anthocyanin; on the other plots, apart from minor fluctuations, the calyx colour was as in the original parent.

Anthyllis vulneraria L.

The final recording of the plants dealt with in the first report was made in the spring of 1930. All the plants were dead, having rotted off from the crown. Autumn and winter seedlings were, in the order of most numerous first: calcareous sand, chalky clay, clay, sand, Potterne soil.

The beds were cleared. Seeds derived from protected and selfed plants on every soil were sown on April 2nd, 1930, raised in heat, in boxes, in the same kinds of soils in which they were pricked out and finally transplanted. Germination occurred in the following order: calcareous sand, sand, chalky clay, clay, Potterne soil. The seedlings (Pl. XV) were transplanted into the beds on May 31st, 1930. On June 3rd, 1930 the sequence of general tone of the seedlings, the best first, was: Potterne soil, calcareous sand, chalky clay, clay, sand. On June 23rd, 1930 the following measurements of length of basal leaves (= radius of seedling plant) were obtained:

Sand: max. 6 cm. (No. 16); min. 4 cm. (No. 25 *a*).

Calcareous sand: max. 8·5 cm. (No. 45), min. 6 cm. (No. 31).
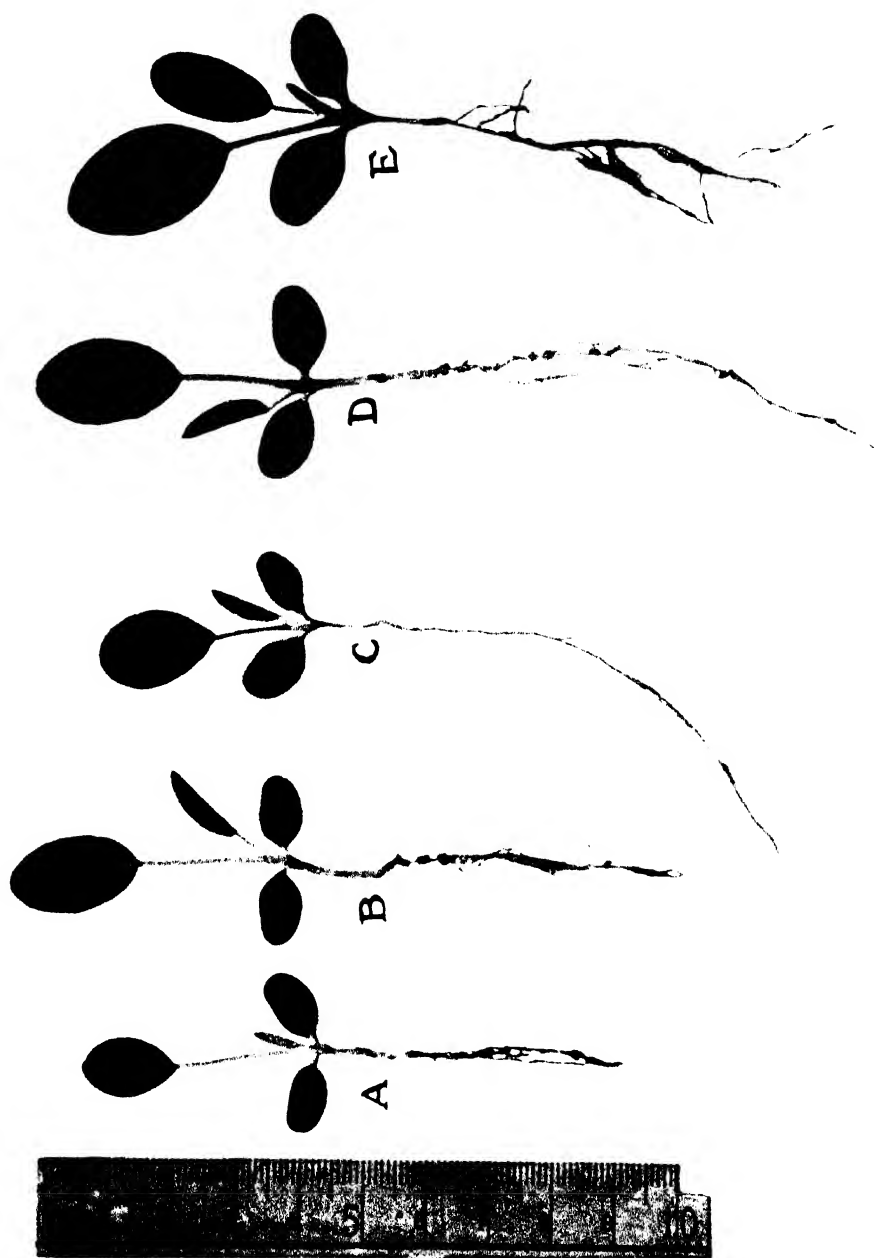
Phot. 2. *Anthyllis vulneraria* seedlings, sown on the stated soil on 2. iv. 1930, collected 4. v. 1930, all on the same date. *A* on sand; *B* on calcareous sand; *C* on clay; *D* on chalky clay; *E* on Potterne soil.

MARSDEN-JONES and TURRILL Report on Transplant Experiments at Potterne

Clay: max. 7 cm. (No. 71), min. 3 cm. (No. 53).

Chalky clay: max. 6 cm. (No. 92), min. 3·5 cm. (No. 100 a).

Potterne soil: max. 11 cm. (No. 147), min. 7 cm. (No. 144).

The seedlings on the last were all much larger and more vigorous than those on any of the other soils. In order of most root nodules first the recording was: chalky clay, calcareous sand, sand, clay, Potterne soil. The record is of seedlings sown on May 4th, 1930, and 29 days old.

For size in first growing seasons the following sequences were recorded, the largest first: August 9th, 1930 and September 10th, 1930, Potterne soil, calcareous sand, clay, chalky clay, sand.

For general tone, September 29th, 1930, the order, best first, was as follows: chalky clay, clay, calcareous sand, Potterne soil, sand.

Deaths in 1930, *i.e. before flowering* (recorded up to October, 1930, i.e. up to 6 months old).

Sand: Nos. 2, 5, 7, 8, 10, 11, 16, 17, 21, 22, 25.

Calcareous sand: 35, 37, 42, 46, 49, 50, 50 a.

Clay: 51, 52, 54, 70, 72, 74.

Chalky clay: 80.

Potterne soil: 129, 134, 135, 137, 138, 142, 143, 144, 145, 147, 148.

All dead plants were replaced by plants of the same age which had been growing on the same soils on October 21st, 1930.

Winter deaths (recorded April 7th, 1931, i.e. 9–12 months old).

Sand: Nos. 4, 6.

Calcareous sand: 40, 44, 45.

Clay: 58, 64, 66, 71, 73.

Chalky clay: 86.

Potterne soil: 126, 127, 128, 130, 136, 137, 149, 150.

These were again replaced, with the exception of those on the Potterne soil.

Spring and early summer deaths (recorded June 20th, 1931, i.e. 12 to 14 months old).

Sand: Nos. 2, 4.

Calcareous sand: 45.

Clay: 73.

Chalky clay: none.

Potterne soil: 131, 134, 139, 140, 141, 142, 143, 146, 150 a.

Summer deaths (recorded July 20th, 1931, i.e. 14 to 15½ months old).

Sand: Nos. 5, 7, 8, 10, 11, 13, 19, 25, 25 a.

Calcareous sand: 29, 31, 33, 35, 36, 37, 41, 42, 44, 46, 47, 48, 49.

Clay: 53, 58, 62, 75.

Chalky clay: 79, 80, 81, 100.

Potterne soil: 125, 132, 133, 148.

Late summer and autumn deaths (recorded December 31st, 1931).

All dead, except five on chalky clay and one on clay, these with only a few green parts the crown having almost completely rotted.

Seedlings.

	27. i. 30	11. v. 30	15. iv. 31	16. v. 31	20. vi. 31	14. viii. 31	31. xii. 31
Sand	Very few	Numerous	Very few	Very few	Few	Few	Very numerous
Calcareous sand	Very numerous	Very numerous	Few	Few	Many	Numerous	Very numerous
Clay	Numerous	Very numerous	Many	Many	Few	Few	Very few
Chalky clay	Many	Very numerous	Few	Few	Few	Very few	Very few
Potterne soil	Few	Numerous	Few	Few	Very few	Very few	None

The continuous germination through spring, summer and autumn of *Anthyllis* seed has been confirmed. That seed may remain dormant, at least for two years, is shown by the figures for 15. iv. 31 and 20. vi. 31. Any germination from seeds which remained longer dormant will be recorded in the future. On the other hand, a proportion of the seed germinates immediately after being shed.

Seed weight and germination.

	Type of soil				
	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil
Mean percentage germination before scarification	14·2	3·5	5·0	9·6	6·2
Mean percentage germination of seeds scarified once only	77·9	72·4	62·6	52·6	58·9
Mean percentage germination of seeds scarified twice	97·6	96·1	96·7	98·6	99·5
Weight of 100 seeds in grams:					
Means	0·421	0·435	0·442	0·425	0·448
Standard deviations	0·027	0·0414	0·0195	0·022	0·048

The differences in germination before scarification are significant. After one scarification seeds from sand again have the highest percentage germination. Practically full germination occurred in seeds from all soils after a second scarification.

The germination tests were made at the Official Seed Testing Station, Cambridge. The seeds were collected at Potterne between July 17th and 23rd, 1929. The germination tests were commenced on 5. iii. 30. The seeds remaining hard were scarified by hand on 24. iii. 30, and the seeds still remaining hard on 2. iv. 30 were again scarified by hand on that day.

General tone (1931), best first.

19. i. 31	15. iv. 31	20. vi. 31
Chalky clay	Chalky clay	Chalky clay
Sand	Sand	Calcareous sand
Calcareous sand	Calcareous sand	Sand
Clay	Clay	Clay
Potterne soil	Potterne soil	Potterne soil

Number of stems per plant.
Sand: max. 75, min. 12, mean 34·4.
Calcareous sand: max. 103, min. 30, mean 64·2.
Clay: max. 62, min. 42, mean 52·2.
Chalky clay: max. 85, min. 47, mean 68·6.
Potterne soil: max. 43, min. 31, mean 38·2.

An analysis of variance showed that the full figures have differences due merely to chance, those within the soils being greater than those between the soils.

Stem heights (recorded 20. vi. 31).
Sand: max. 5·6 dm. (No. 14), min. 2·8 dm. (No. 5).
Calcareous sand: max. 6 dm. (No. 36), min. 3·7 dm. (No. 50).
Clay: max. 4·3 dm. (No. 75), min. 1·4 dm. (No. 71).
Chalky clay: max. 6·2 dm. (No. 83), min. 3·8 dm. (No. 80).
Potterne soil: max. 3·6 dm. (No. 138), min. 3 dm. (No. 129).

The number of flower heads was up to 5 per stem (mostly 3–4) on clay and Potterne soil; on sands and chalky clay up to 6 (mostly 4–5).

Number of flowers per head.

	Sand	Calcareous sand	Clay	Chalky clay	Potterne soil	Totals
Means	20·47	19·37	16·05	21·87	14·87	18·525
Standard deviations	2·80	3·19	2·43	2·01	2·69	—

The differences between the means have been tested by a process of analysis of variance and a z test and were found to be significant. The standard error of any mean is 0·33, and a difference of more than three times this is significant, thus all differences between pairs of the above means are significant, that between sand and calcareous sand only just so [Fisher: *Statistical Methods for Research Workers*, p. 194 (Edinburgh and London, 1928); Fisher and Wishart, *Imp. Bur. Soil Science*, Technical Communication No. 10, p. 15 (London, 1930)].

Primary flowering. Compared with the graph on p. 373 of the first report the most constant feature is the relative precocity of flowering on the calcareous sand. On the well drained sand the plants flowered relatively earlier in 1931 than in 1929.

Florifery (recorded June 20th, 1931). The order, most floriferous first, was: chalky clay, calcareous sand, sand, clay, Potterne soil.

Completion of primary flowering. The order of completion of flowering was: calcareous sand, sand, Potterne soil, chalky clay, clay.

Secondary flowering from lateral shoots (recorded July 20th, 1931): sand 15 plants; calcareous sand 6; clay 19; chalky clay 19; Potterne soil 5.

Plasticity. Anthyllis was not morphologically plastic on any of the soils. Except for the fluctuations in size and numbers of flowers per head recorded above it remained true to parental type.

19-2

Plantago major L.

Winter condition and deaths. The species is normally a rosette hemicryptophyte. The majority of the leaves die off in autumn, the young ones in the centre of each crown alone remaining green to form the perennial bud. In

PRIMARY FLOWERING. PLANTS IN FLOWER, 1931.
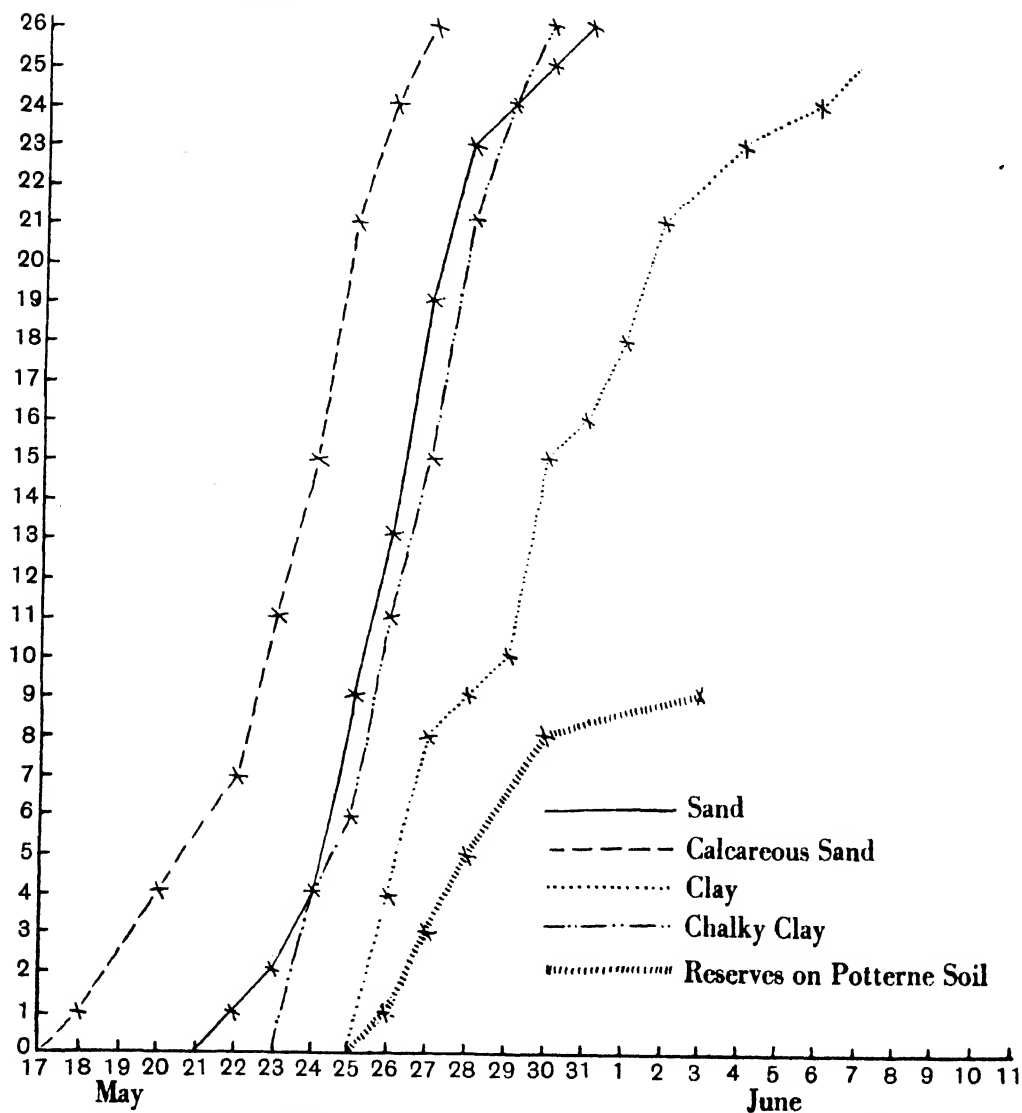
FIG. 4. *Anthyllis vulneraria.* Graph showing numbers of plants in flower (ordinates) plotted against dates (abscissae).

old plants the crowns multiply by branching, especially on the clays and Potterne soil.

Deaths in the winter 1929–30 (about 9 months old) occurred as follows: sand Nos. 4, 5, 9, 10, 17, 19, 24, 25; calcareous sand No. 30; clay none; chalky clay none; Potterne soil Nos. 129, 135, 138.

During the summer of 1930 (i.e. 12 to 16 months old), on Potterne soil Nos. 127, 130, 141 died.

In the winter 1930–1 deaths (of plants $1\frac{1}{2}$–2 years old) occurred as follows: sand Nos. 2, 7, 22, 23; calcareous sand Nos. 27, 28, 29, 32, 35, 39, 40, 42, 43, 44, 45, 48, 49, 50; clay none; chalky clay none. Nos. 27, 28, 29, 30, 32 on calcareous sand were replaced on April 7th, 1931 by plants of same stock and age which had been grown on the same soil. All dead plants on sand and Potterne soil were replaced by seedlings grown from seed obtained from protected and selfed original transplants on each of these soils.

Summer and autumn deaths 1931: sand Nos. 21 ($2\frac{1}{2}$ years old), 25 (6 months old); calcareous sand (up to $2\frac{1}{2}$ years old) Nos. 34, 36, 37, 46; clay, none; chalky clay (up to $2\frac{1}{2}$ years old) Nos. 77, 79, 80, 81, 82, 83, 84, 85, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100; Potterne soil, none.

Plants on calcareous sand and chalky clay were protected and selfed in 1931 to obtain seed for replacement of losses.

Diseases, etc. Ramularia plantaginea attacked the plants in 1931. It appeared on all the beds but was very virulent on the chalky clay where it caused the leaves to wither, brown off and die. The loss of almost the entire stock on the chalky clay was apparently due to the death of the foliage accentuated by slug attack. On the clay (31. xii. 31) many of the much divided crowns, especially the central ones, rotted loose but had living central shoots from which adventitious roots were developing. This appears to be a means of vegetative multiplication.

On sand, calcareous sand, reserves, and at Kew the plants all heaved up above the soil after frost and had to be replanted. On the clay and chalky clay there was little or no heaving up by frost.

Seedlings.

	Spring seedlings			Autumn seedlings
	15. iv. 31	16. v. 31	22. vi. 31	31. xii. 31
Sand	Numerous	Very numerous	Very numerous	None
Calcareous sand	None	Very few	2	None
Clay	Few	Few	Few	None
Chalky soil	Numerous	Numerous	Very numerous	None
Potterne soil	Numerous	Many	5	None

On the Kew soil spring seedlings were numerous. It appears that germination in this species is limited to the spring and is nearly simultaneous.

General tone (apart from deaths) in order of best first:

27. i. 30	10. ix. 30	15. iv. 31	16. v. 31	22. vi. 31	14. viii. 31
Clay	Clay	Clay	Clay	Clay	Clay
Potterne soil	Chalky clay	Chalky clay	Chalky clay	Chalky clay	Potterne soil
Chalky clay	Sand	Sand	Potterne soil	Sand	Sand
Sand	Calcareous sand	Calcareous sand	Sand	Calcareous sand	Chalky clay
Calcareous sand	Potterne soil	Potterne soil	Calcareous sand	Potterne soil	Calcareous sand

Habit. Certain plants developed a "strict" habit, the leaves growing practically erect. On June 3rd, 1930 this was recorded for sand No. 7, calcareous sand Nos. 29, 34, 44, chalky clay No. 88. On August 9th, 1930, Nos. 7, 44, 88 retained the "strict" habit, and on chalky clay all the remaining plants were showing a tendency to become "strict," except Nos. 78, 80, 81, 84, 85, 92, 95.

On June 22nd, 1931, the habits recorded were: sand, all flat except No. 15 which was becoming "strict"; calcareous sand, all flat except Nos. 26, 27, 31 and 34 which were more or less "strict"; clay, all flat except Nos. 56, 71, 72, which had some new leaves erect; chalky clay, all "strict" except No. 78 which was flat; Potterne soil, all (4 old plants alive) flat.

Indumentum (recorded June 22nd, 1931).

Sand: spreading hairs on peduncles Nos. 1, 6, 8, 11, 13, 21, i.e. all that were in flower.

Calcareous sand: spreading hairs on peduncles Nos. 26, 27, 29, 32, 33, 38, 41, 47, i.e. all that were in flower.

Clay: adpressed hairs on peduncles of all plants, except Nos. 65, 69 where slightly spreading hairs occurred in lower half.

Chalky clay: adpressed hairs on peduncles of all plants. On the clays the peduncles all tend to become glabrescent in the lower half where hidden among the leaves and to have completely adpressed hairs in upper half.

Potterne soil: indumentum spreading on peduncles in Nos. 126, 128, 132, 133.

Diameters and heights.

June 3rd, 1930.

    Sand: max. 8·5 cm. (No. 21), min. 1·5 cm. (No. 17).

    Calcareous sand: max. 13 cm. (No. 50), min. 5·7 cm. (No. 39).

    Clay: max. 36 cm. (No. 71), min. 21 cm. (No. 52).

    Chalky clay: max. 24·5 cm. (No. 95), min. 11·5 cm. (No. 80).

    Potterne soil: max. 20 cm. (No. 128), min. 11 cm. (No. 133).

June 23rd, 1930.

    Sand: max. 10·5 cm. (No. 21), min. 2 cm. (No. 17).

    Calcareous sand: max. 14 cm. (No. 50), min. 7·5 cm. (No. 30).

    Clay: max. 48 cm. (No. 71), min. 26·5 cm. (No. 52).

    Chalky clay: max. 30·1 cm. (No. 95), min. 16 cm. (No. 80).

    Potterne soil: max. 22 cm. (No. 128), min. 9 cm. (No. 133).

    "Strict" plants: No. 7, 5·5 cm. high; No. 29, 4 cm. high; No. 88, 17 cm high.

June 22nd, 1931.

    Sand: max. 20 cm. (No. 8), min. 5·5 cm. (No. 3).

    Calcareous sand: max. 11 cm. (No. 29), min. 3 cm. (No. 43).

    Clay: max. 54 cm. (No. 60), min. 23 cm. (No. 63).

Chalky clay: No. 78, 28 cm. (other plants "strict").

Potterne soil: max. 29 cm. (No. 133), min. 20 cm. (No. 126).

"Strict" plants: max. (No. 79), 18 cm. high, 35 cm. spread; min. (No. 96), 9·5 cm. high, 12 cm. spread.

August 14th, 1931.

Sand: max. 24 cm. (No. 8), min. 10 cm. (No. 3).

Calcareous sand: max. 15 cm. (No. 29), min. 43 cm. (No. 7).

Clay: max. 60 cm. (No. 60), min. 19·6 cm. (No. 63).

Chalky clay: No. 78, 33 cm. (other plants "strict").

Potterne soil: max. 27 cm. (No. 133), min. 22 cm. (No. 132).

"Strict" plants: max. (No. 79) 16 cm. high, 37 cm. spread; min. (No. 96) 9 cm. high, 16 cm. spread.

Length of inflorescences.

Clay.

No. 62 (max.) spike + peduncle 3 dm., spike 1·9 dm.

No. 61 (min.) spike + peduncle 1·15 dm., spike 0·65 dm.

Chalky clay.

No. 86 (max.) spike + peduncle 2·65 dm., spike 1·45 dm.

No. 80 (min.) spike + peduncle 0·45 dm . spike 0·25 dm.

Upright plant No. 88 (max.) spike + peduncle 2·95 dm., spike 1·45 dm.; (min.) spike + peduncle 1·7 dm., spike 1·0 dm.

Calcareous sand.

No. 28 (max.) spike + peduncle 0·75 dm., spike 0·42 dm.

No. 43 (min.) spike + peduncle 0·1 dm., spike 0·06 dm.

Sand.

No. 21 (max.) spike + peduncle 1·07 dm., spike 0·7 dm.

No. 17 (min.) spike + peduncle 0·45 dm., spike 0·25 dm.

Potterne soil.

No. 128 (max.) spike + peduncle 2·65 dm., spike 1·17 dm.

No. 132 (min.) spike + peduncle 0·85 dm., spike 0·4 dm.

Florifery. Except on one plant on each soil all inflorescences were cut off before the seeds were dispersed. In 1930 three records were made of numbers of inflorescences. At the first and second records, July 23rd and September 10th, plants on all soils produced inflorescences. On November 25th only plants on clay and chalky clay had inflorescences. In 1931 records on July 10th and September 25th gave inflorescences on all soils, but in November no more inflorescences had been produced on any soils.

Only two seedlings raised from a protected selfed plant on sand flowered the same year, whereas on the Potterne soil all seedlings flowered the same year. Self-sown seedlings (14. viii. 31) on sand and calcareous sand did not flower, on clay six flowered, on chalky clay three flowered, on Potterne soil most flowered.

In general inflorescences were more nearly erect on the clays than on the sands.

Spikes per plant.

	Sand		Calcareous sand		Clay		Chalky clay	
	1930	1931	1930	1931	1930	1931	1930	1931
Maximum	19	30	10	13	195	230	104	70
Minimum	4	0	0	0	46	21	18	4
Mean	11·65	14·86	3·48	6·33	102	81·2	64·64	24·36
Standard deviation	4·1	8·3	3·4	3·8	34	44	23	15

In preparing the above Table dead plants have been omitted entirely. The figure 0 indicates that the plant was alive but produced no spikes. The great differences between sands and clays are too obvious to need comment at the present stage of the experiments.

Primary flowering. The wide range of the flowering periods prevent the graphical representation of this character in a manner similar to that used for other transplants. We therefore give the figures in tabular form. The earlier flowering of the plants on the clays is most marked for both seasons.

Primary flowering
Numbers of plants in flower

		1930				1931			
		Sand	Calcareous sand	Clay	Chalky clay	Sand	Calcareous sand	Clay	Chalky clay
May	30	—	—	—	—	—	—	1	—
„	31	—	—	—	—	—	—	1	—
June	1	—	—	1	—	—	—	1	—
„	2	—	—	1	—	—	—	1	—
„	3	—	—	2	—	—	—	4	3
„	4	—	—	4	1	—	—	5	3
„	5	—	—	5	1	—	—	5	3
„	6	—	—	5	1	—	—	6	3
„	7	—	—	5	1	—	—	7	4
„	8	—	—	6	2	—	—	7	5
„	9	—	—	7	3	—	—	7	5
„	10	—	—	7	4	—	—	7	5
„	11	—	—	7	4	—	—	8	5
„	12	—	—	9	5	1	—	9	5
„	13	—	—	10	5	1	—	12	5
„	14	—	—	11	8	2	—	13	5
„	15	—	—	13	8	2	—	14	7
„	16	—	—	13	10	2	—	16	8
„	17	—	—	20	20	2	—	16	9
„	18	—	—	22	22	2	—	18	12
„	19	—	—	22	22	2	—	19	13
„	20	—	—	23	23	2	—	23	16
„	21	1	2	25	24	2	—	24	19
„	22	1	2	—	25	4	2	—	21
„	23	1	4	—	—	5	3	—	22
„	24	1	5	—	—	5	5	—	22
„	25	2	5	—	—	6	5	—	23
„	26	3	6	—	—	6	6	—	—
„	27	3	7	—	—	6	6	—	—
„	28	3	9	—	—	8	8	—	—
„	29	3	9	—	—	8	—	—	—
„	30	3	9	—	—	8	—	—	—
July	1	3	10	—	—	10	—	—	—
„	2	5	10	—	—	10	—	—	—

Primary flowering
Numbers of plants in flower

		1930				1931		
	Sand	Cal-careous sand	Clay	Chalky clay	Sand	Cal-careous sand	Clay	Chalky clay
July 3	6	15	—	—	10	—	—	—
,, 4	7	17	—	—	10	—	—	—
,, 5	9	17	—	—	11	—	—	—
,, 6	10	18	—	—	—	—	—	—
,, 7	12	18	—	—	—	—	—	—
,, 8	12	18	—	—	—	—	—	—
,, 9	13	21	—	—	—	—	—	—
,, 10	13	24	—	—	—	—	—	—
,, 11	15	—	—	—	—	—	—	—
,, 12	16	—	—	—	—	—	—	—
,, 20	17	—	—	—	—	—	—	—
,, 21	18	—	—	—	—	—	—	—

SUMMARY AND TENTATIVE CONCLUSIONS.

1. The figures for rainfall, temperature, and humidity are given for 1930 and 1931 and for rainfall also for November and December, 1929. Although the annual total rainfall was not markedly excessive the absence of any considerable hot dry summer weather undoubtedly acted adversely on many of the plants, increasing the amount of damping off and the damage done by slugs.

2. The results of periodic records of the five species for the two years are embodied in this report. The chief facts which have emerged are:

Centaurea nemoralis. This is decidedly the most persistent perennial (on our soils) of the five species. Deaths and reduction in size through smothering by its own débris has been marked, especially on the clays. A fairy-ring-like growth of individual plants is becoming evident. On the sands and chalky clay the plants were lighter in colour, through the development of somewhat shorter and less numerous hairs, than plants on clay and Potterne soil.

Silene vulgaris. The "strict" habit which at first showed itself in the plants on calcareous sand, became much less marked in 1930 and had almost disappeared in 1931. Plants on the clay retained and intensified the lighter (yellowish green) colour of the vegetative parts. The foliage colour on the other soils became practically stabilised to that of the original parent. General tone became best on chalky clay and worst on sand. On all soils germination of seeds was again limited to the spring. On clay the main roots spread nearly horizontally. On the remaining soils they penetrated nearly vertically, but were much coiled immediately below the root-stock on the Potterne soil. The superficial cells of the older roots were coloured differently in the various soils. On none of the soils did *S. vulgaris* develop characteristics of *S. maritima* or vice versa.

Silene maritima. On the sand the plants retained the smaller leaves and greater amount of anthocyanin already recorded, and smaller leaves also again

appeared on the calcareous sand. On the clay as the plants became older they became more woody, with elongated stems bare of leaves for considerable distances towards the crown, as contrasted with plants on the other soils. On the chalky clay the parental habit was retained. Plants on all soils, with the exception of those on the Potterne soil, showed rooting at the nodes. Both spring and autumn germination of seeds occurred. Seedlings germinated best on the calcareous soils in 1930 and on the calcareous sand in 1931. In general the plants did best on chalky clay till the sudden deaths of all except one in 1931.

Anthyllis vulneraria. Again no morphological changes of a qualitative nature occurred in the new stock. The seedling development was quickest on Potterne soil, but at maximum flowering period the plants on the calcareous soil were of much better tone than those on the non-calcareous soils. There is continuous germination of seeds through all the year, except during hard frost. Although *Anthyllis* is probably a relatively persistent natural crop, under experimental conditions, such that individual plants have no competition, growth becomes so luxuriant that the great output of seed results in impoverishment, and dense growth leads to rotting of the crowns and death.

Plantago major. The very great differences between the plants on the various soils has been increased. On the sands the plants have remained small; on the clays they made most luxuriant growth. The significance of these differences is well shown by the measurements and counts given. A peculiar "strict" habit, with the leaves growing practically erect, developed in all plants, except one, on the chalky clay, and some tendency towards this strict habit was observed on the calcareous sand. On the sands and Potterne soil the peduncles produced spreading hairs; on the clays the peduncles were glabrescent below and had adpressed hairs on the upper part. On the sands the plants heaved up after frost. This did not occur on the other soils.

3. In 1931 a biotic factor was introduced by the occurrence and multiplication of slugs on the clays. In both the years here reviewed mosses increased very considerably on the bare places of the soils and even threatened to compete with the transplants on the calcareous sand.

4. Apart from the quantitative and qualitative changes on the different soils the accurate recording of mortality and behaviour during different stages of life-history are providing data of an ecological nature.

5. Continued work on the experiments has impressed us with the very different reactions, or lack of reactions, of the species being used and with the complexity of a plant's environment. It is impossible, except on the basis of empirical knowledge of a given species, to foretell how that species will react to such conditions as those under which the transplant experiments are being conducted. The degree and nature of plasticity are inherent "characters." It was the original intention of the committee to experiment with the influence of edaphic factors on the species chosen, other factors being kept uniform,

but the plants being grown as naturally as possible. The event has proved this an impossible ideal under the given conditions. The interaction of factors is so great that a complete study of their individual action could only be undertaken by very considerable extension of the experiments. The direct influence of the physical and chemical peculiarities of the soils on the characters of the plants has been our chief concern, but this influence has frequently proved indirect, varying with climatic factors and sometimes acting through biotic factors.

[Mr. C. G. T. Morison's account of the soils used in these experiments on pp. 475-8 of this issue is to be considered as part of this Report].

VEGETATION TYPES IN GODTHAAB FJORD

IN RELATION TO THOSE IN OTHER PARTS OF WEST GREENLAND, AND WITH SPECIAL REFERENCE TO ISERSIUTILIK

By C. G. TRAPNELL.

(With Plates XVI–XXI and one Map in the Text.)

CONTENTS.

I. INTRODUCTION.

(1) *Field work (see map).*

IN June of 1928, through the courtesy of the Government of Greenland, the Oxford University Greenland Expedition established a base camp at Isersiutilik, in the Kugssuk inlet of Godthaab Fjord, 40 miles inland north-east of Godthaab (Isersiutilik, lat. 64° 40′ N., long. 51° 20′ W.; Godthaab, lat. 64° 11′ N., long. 51° 45′ W.; admiralty charts 235–76). The Kugssuk inlet was biologically unexplored except for some botanical observations by Vahl and Rink, cited by Rosendahl (**35**) and others. A Danish meteorological station recorded at Kornok (more correctly Qôrnoq, lat. 64° 26′ N., long. 50° 58′ W.) from 1882 to 1891. The only other observations of consequence were those made by Nansen on climate and physiography in Godthaab Fjord (**9**).

The object to which the whole expedition was devoted was the making of an ecological survey of a typical sample area, about 10 square miles in extent, of the interior of the western land belt. Isersiutilik was chosen as topographically most suitable, and how typical it proved will be seen from
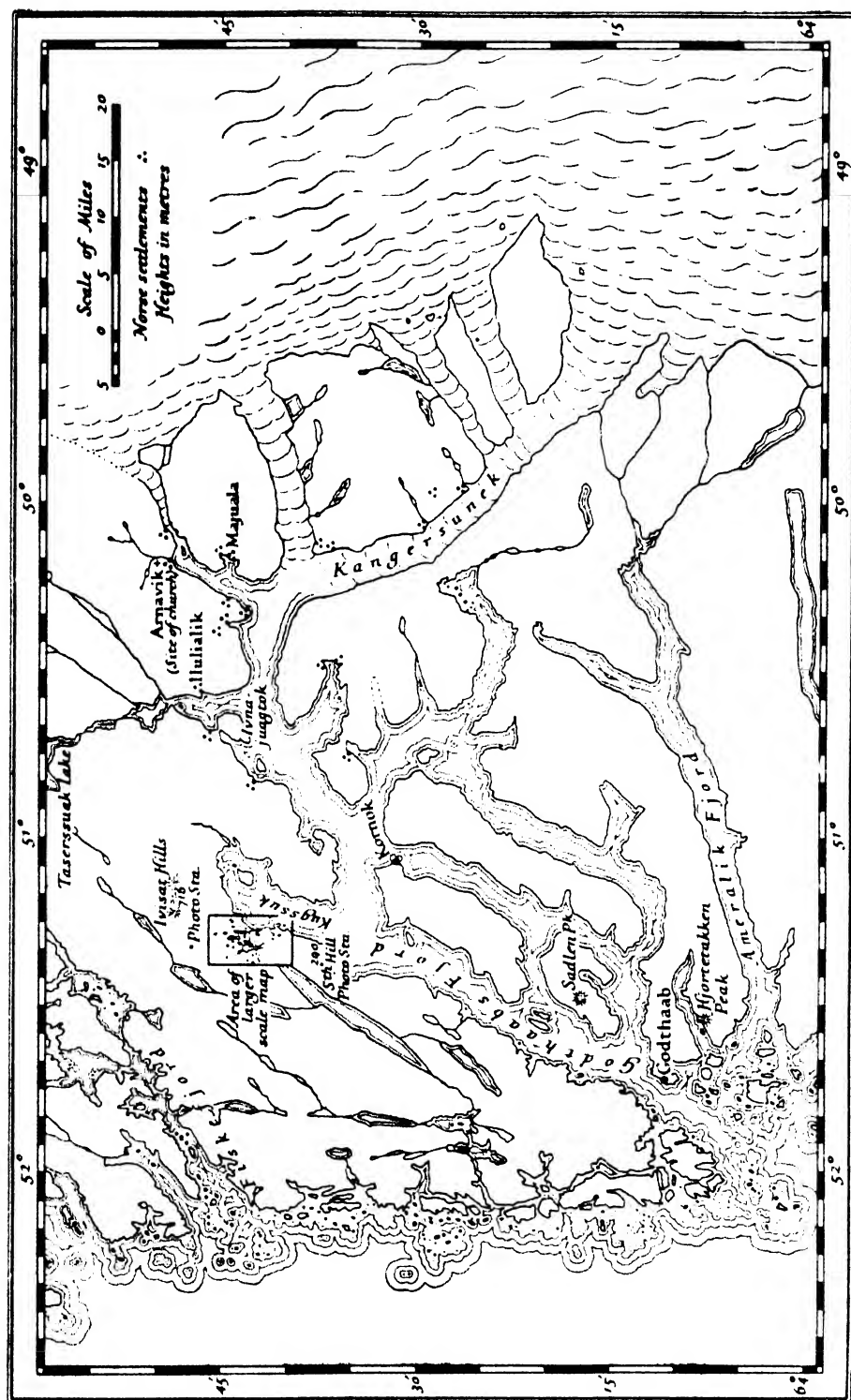
Fig. 1. Godthaab Fjord. Reproduced by courtesy of the Royal Geographical Society.

the present paper. A topographic survey was made of the area (see Longstaff (**7**)), the Kornok station being relied on for meteorological data. In conjunction with the vegetation survey samples of representative soils were examined, and field determinations of hydrogen-ion concentration checked subsequently in England. Soil micro-organisms were not studied, since they have already been well analysed for the Disco region. The plankton of lakes above pond size was necessarily left untouched save for sampling of the diatom population (see Fuge (**38**)). The zoological work comprised an analysis of the insect population and a census of the bird population, involving the mapping of every nest over 8·4 square miles. In this connection entomological and botanical analyses were made of the stomach contents of over 100 birds brought back to England, and from these will be worked out the food requirements of the 727 pairs of 14 species located on the area by the ornithologists.

The Isersiutilik survey was combined with reconnaissance in various parts of the fjord, observations on altitudinal transects being made at intervals of 100 ft. by the aneroid.

Botanical observations were carried out as follows:

Maritime region. Rough primary survey of the small Godthaab peninsular (some 2 square miles), June 15th and August 2nd, supplemented by field glass observations of the fjord slopes inland on June 16th and August 1st.

Subcontinental region. Survey of the Isersiutilik area and its neighbourhood, about 10 square miles, June 16th to July 4th, July 9th to August 1st, with reconnaissances about Kugssuk, assisted by T. G. L., E. M. N. and J. H. and a route transect in the Ivisat foothills. Altitude transects comprised two ascents of the Ivisat hills, one of Nugarssuk bird cliff and one of South Hill, and various supplementary reconnaissances were made.

Continental region. Reconnaissances at the west entry of Ujaragssuit, June 18th, Majuala, July 5th to 6th, Ilulialik, July 6th to 7th, with field glass observations of the fjord slopes between these points and landings nearer Kugssuk. One altitude transect was made at Ilulialik, and supplementary observations by E. M. N. and T. G. L.

Reconnaissance was thus necessarily rapid, and could only be carried out by means of the "local types" analysed in section III (1) and by observations on growth type and frequency of dominant species. The validity of the local types employed requires to be tested by subsequent expeditions, but it is hoped that inaccuracies have been avoided by repeated confirmation from Rosenvinge (**51**) and other authors. Species identified by eye are queried whenever there is any grounds of doubt, the one serious case being the possibility of confusion between *Alectoria nigricans* and *Parmelia pubescens* in certain situations.

The primary object of this paper is to determine the environmental relationships of the dominant species and local types found at Isersiutilik by studying their recurrence in other parts of the fjord and on the west coast

generally. It is therefore largely a summary of reconnaissance results, supplemented by citations from other accounts of the west coast. At the same time it is hoped to show by this means the relation of the Isersiutilik survey to ecological surveys made on previous Oxford expeditions to the Spitsbergen archipelago and on subsequent expeditions of the Oxford University Exploration Club to Lapland and Hudson Strait.

The vegetation is described on the basis of climatic and physiographic "regimes," the description of the subcontinental "low fjaeld" of Isersiutilik being in each case reserved to the last. Only these two main groups of factors are considered, the reason for this lying in the extent of the area considered. The treatment is best made clear by definition:

(1) *Regional aspect.* Environment and vegetation are considered in so far as they show constant characteristics over large areas. Broad vegetation types are here dependent on external factors, physical factors of the environment unmodified by the organisms they control. These factors fall into two groups, *climatic* and *physiographic*, the latter term being here used to include the geology. For practical purposes these groups may here be treated as independent, except in so far as the climate is modified by the physiography, leading to what is here termed *orographic variation*. The vegetation type determined by such a regime is termed the *regional type*.

(2) *Local aspect.* Environment and vegetation are considered over small areas. Here the vegetation is in the first instance determined by *sites* whose characteristics arise from the interaction of climate and physiography, namely the *microclimate* and the *geomorphology*. In these parts, owing to the very slight normal erosion and the great influence of aspect and snow cover, these lesser external factors are of paramount importance in differentiating vegetation types, internal factors being slight in effect. The term geomorphology is used to cover microrelief, subsoil structure and drainage, being the static aspect of Tansley's geodynamic factor. Vegetation types determined by these factors of site are referred to as *local types*.

(3) *Internal aspect.* The organisms themselves and the set of modified conditions they produce in their environment are here termed *internal factors*. Those concerned are the abiotic factors of plant-modified climate and of plant- and animal-modified soil[1], and the causal organisms, treated as phytobiotic and zoobiotic factors. The set of conditions set up by these factors in combination may perhaps be termed the *biome*, and the community which the organisms collectively constitute, the *biocoenose* or *biotic community*. Such a community of course falls within the sphere of influence of external factors, and may be described either on a regional or a local basis.

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[1] It will be observed that on this classification of factors the term edaphic factor has to be discarded as an ambiguous one, covering both internal and external soil factors. This is done the more readily here in that the soil is of an "immature" type consisting of a layer of humus over a little modified substratum.

In the present account only the regional aspect is dealt with, though the local aspect has to be referred to owing to the great local variation found within any one region. In a subsequent joint account of the plant and animal communities of Isersiutilik, the local aspect will be dealt with, in conjunction with the internal aspect, in greater detail.

The necessity of constant reference to the local aspect will be seen from the account of the vegetation. In a general way the sparse green and mossy heath of the coastal lowlands could be seen gradually increasing in luxuriance inland, with the inclusion of yellow lichen patches in the tangle, till, in the innermost recesses of the land-belt, areas of drier lichen heath with sparser or more matted shrubs again began to appear. Floristic and habit changes were also noted. But to define the changes beyond this rather vague description it is necessary to employ the local type as the one recognisable unit of vegetation classification (compare the section on Classification, p. 307). The reason for this is that under the influence of the geomorphology and of the winds and the low sun on the depth and duration of the snow cover, the frequencies of species and the whole facies of the heath changes in a kaleidoscopic fashion over small areas.

From the interaction of these various microclimatic and geomorphic factors there arises in fact an enormous multiplicity of habitats. If two to four grades are taken for each of the factors of snow depth, snow duration, snow flushing, ground water and soil texture, the number of theoretically possible combinations is more than can be coped with. The combinations actually found would require prolonged investigation and over-wintering on the spot for their full elucidation, by such a method as that discussed in a previous note (13). The apparent confusion is intensified by competition between little specialised species, especially between dwarf shrubs whose root development is enormous for the shallow soil, and between them and great numbers of lichens and bryophytes. Where a transition also takes place between regional types, as at Isersiutilik, with its balance between dwarf shrubs, mosses and lichens, the striking patchwork so formed frequently breaks down into bewilderingly heterogeneous vegetation, with complete lack of dominance either of species or life form. But though much of such heath is a mixture of species of varied environmental affinities, the component groups of species become clearer wherever the balance of factors is sufficiently altered in one direction.

By working on these more extreme sites the multifarious heath population of Isersiutilik was listed under 13 communities of 15 to 40 species each. The number may appear large, but it must be borne in mind that it was possible to pass in a matter of paces from diminutive "high arctic" species to boreal species in scrub that stood above one's head. The physiognomy of these associations and their chief species were correlated with types seen on reconnaissance work in other parts of the fjord, and from these observations were defined the local types given in the section on classification. Local types may

vary both in the number of associates represented and in the area occupied, the latter ranging from a few square feet to many acres according to conditions. Their widespread recurrence with replication of the same conditions may be gauged from the fact that while 13 types were determined at Isersiutilik, only 16 were noted for the whole fjord lowlands. These types represent those which were recognised as significant, but others might well be found in the same region. What types are selected is largely a matter of convenience or ease of recognition. The essential thing was to provide a system of classification sufficiently elastic to cope with the local variation described.

(2) *Acknowledgments.*

Salix:	B. Floderus.
Taraxacum:	H. Dahlstedt.
Draba:	O. E. Schulz.

Euphrasia: H. W. Pugsley.
Empetrum: O. Hagerup.
Gramineae: A. W. Hubbard and O. R. Holmberg.
Erigeron, etc.: J. Lid.
Hieracium: E. Almquist.

Pteridophytes: Royal Botanic Gardens, Kew (C. H. Wright).
Mosses: H. N. Dixon.
Hepatics: W. Watson and H. H. Knight.
Lichens: R. Paulson.
Fungi: E. M. Wakefield.
Diatoms: D. P. Fuge.
Other algae: N. Carter.
Miscellaneous plants: Botanical Dept., British Museum (Nat. Hist.).
Bryozoa: O. Nordgard.
Peat analyses: K. Jessen (preliminary examination: G. Erdtman).
Rock samples: Minerals Dept., British Museum (Nat. Hist.).
*p*H values: School of Rural Economy, Oxford.

Much valuable help concerning the soils was given by Mr E. M. Crowther and others of the chemistry department of Rothamsted Experimental Station, and facilities for the examination of their Greenland material were provided by the herbaria of Kew, Copenhagen and Stockholm. To the members of these institutions I wish to express my thanks for their advice and assistance.

Finally, I wish to express my gratitude to those whose advice has guided the production of this paper, and in particular to Prof. A. G. Tansley and Mr V. S. Summerhayes for much helpful criticism.

II. Environment.

(1) *Climatic regimes.*

The following preliminary attempt to group West Greenland climatic regimes employs the available temperature records for the summer (frost-free) season, the bitter winter temperatures appearing similar in their effects throughout the country: in general removal of snow cover appears to be fatal to a large number of species everywhere, for in the very great winter range of absolute temperature (40–50° C. in January, maxima commonly exceeding the July mean) such plants, reawakened by the sudden spells of warmth, are liable to desiccation when the cold winds return. Accordingly the July means are used, with the 10° C. July isotherm taken as the approximate limit of the Arctic; its close relation to the limit of woodland has been frequently noticed (cf. Lündegårdh (**8**)), and is well shown in two graphs cited by Haviland (**5**) for tundra and taiga; but it is, of course, clear that a complex of factors has really to be considered, and reference should be made to the formula devised for the limit by O. Nordenskjold (**28**). More satisfactory figures are probably

temperature totals—the sum of positive monthly mean temperatures multiplied by the number of days of the frost-free period. These are also estimated, but to be strictly comparable the sums of means should be multiplied by the actual duration of daylight, calculated in days, the reason being that the apparent decrease in length of the summer season with increasing latitude is partly compensated for by increasing length of day, with reduction, and final disappearance, of night radiation losses.

Although temperatures are employed in their definition, the selection of the regimes is based as far as possible on the wind systems and the distribution of coastal fog. In this respect data are insufficient for the Polar and High Arctic regimes described. They appear to be most sheltered and fog-free inland, and may ultimately be subdivisible into maritime and continental regimes after the manner of Summerhayes and Elton (**66**).

It should be noted that the July mean shows little correlation with the decrease in angle of insolation northwards. In the interior the ice-cap winds warmed by compression, and on the coast the cold fog and sea winds, lead to the distribution of temperature regions being roughly parallel with coast and ice-cap. The effect on the coast is such that Nanortialik has actually a colder July than Godthaab, while, inland, Kornok was if anything cooler then than some stations in Umanak Fjord during the periods of observation. But precipitation decreases rapidly northwards and inland, while Baur (**17**) shows the coast to have a comparatively fog-free region between Holstenborg and Umanak Fjord.

The following four climatic regimes are distinguished:

Polar regime of high pressure conditions, with minimal snowfall, partly evaporating before the thaw: temperature total under 1500, and falling as low as 390: July mean under 5° C. *Stations:* Lady Franklin Bay, North Star Bay, Inglefield Bay. (Cf. Koch regarding wind conditions and coastal fog (**22**), and Baur *passim* (**17**).)

High Arctic regime of glacial winds of the ice-margin, arid (precipitation under 20 cm.), with light snowfall: temperature totals between 1500 and 3000, and July means between 5 and 7·5° C. *Stations:* some in Umanak Fjord; of others, Jacobshavn represents transitions to Low Arctic conditions, while Upernivik is reckoned as on the edge of the Polar regime. (Cf. Baur (**17**) and Petersen (**21**).)

Maritime Arctic regime of the coast south of Disco Bay or Holstenborg, subject to humid south-westers of depressions moving up Davis Strait and to fog condensed by the cold polar current flowing north from Cape Farewell: the effect of this current ceases soon after Holstenborg, while the effect of the south-westers falls off with the passing of the Sukkertoppen ice arm in the same region. The winter winds are chiefly from the ice cap, at Godthaab the north-easter, known to the Esquimaux as Tamaké, "the wind that blows down the fjord." Humid climate (precipitation over 50 cm.), with ample

winter snow cover, frequently lying over a metre in depth and disappearing late, between May and July. During the cloudy summer pack-ice is brought to the Godthaab skerries about July, when the relative humidity rises sharply, while the fog associated with it rises from a minimum of 0·2 days per month in January to maxima of 13 days in July and August. Consequently there is a considerable lowering of insolation and of the intensity of chemically active light, investigated elsewhere by Porsild (**18**). July means between 5 and 7·5° C., and temperature totals between 3000 and 5000. *Typical stations:* Godthaab and Nanortialik. (Cf. Petersen (**21**), and comments in Rosenvinge (**51**), supplemented by verbal information quoted in the introduction, figures in Krabbe (**6**) and data from the *Arctic Pilot* (**16**).) The distance inland for which the regime is held to extend is best determined by the extent of influence of predominant summer sea winds.

Low Arctic regime of the continental belt inland of the last, the "warm, dry steppe region" of O. Nordenskjold (**27**). The dry winds of the glacial anticyclone predominate not only in winter, as north-easters in Godthaab Fjord, but also in summer as warm south-easters of great regularity, though a cold sunset wind was experienced close to the ice. The conditions on the average are semi-arid, the precipitation of 20–50 cm. being borne inland from the sea except for local condensation showers, and largely collected by seaward mountains. The subcontinental regions of the south-west are probably more humid, but the southward increase in precipitation may be accompanied by an increase in evaporation due to the higher temperatures. With the probable exception of the same regions the snow cover is typically shallow (measurements under 30 cm.), and the more so in that sudden "warm waves" occur in mid-winter and "foehns," sometimes of enormous velocity, accompany considerable rise of temperature and remove much, and even all, of the snow: the remainder is described as mostly disappearing in March and April. The summer insolation is intense, the July mean of 7·5–10° C. giving no fair measure of the sun's power, a qualification which, to judge from the figures of Wulff (**22**) and others, may also apply to the continental Polar and High Arctic regimes. Temperature totals range from 3000 to at least 8000. (Cf. Kornok data below, Petersen (**21**), Rosenvinge (**51**), Nansen (**9**) and supplementary information on winter factors from Messrs Church and Bangsted.) The upper limit of the July mean in the south is actually unascertained, and stations by the cold waters of the south-western fjords, which act as funnels for the sea winds, cannot be expected to represent it. 2° C. may be the minimum difference between the coast and the continental region, increasing in the extreme south where there is an approach to high boreal conditions (*vide* (**51**)).

Isersiutilik. The expedition's surveyed area falls in the subcontinental region of Godthaab Fjord and in the Low Arctic regime as described, its climate, except for a possibly greater amount of sun, being fairly represented

by the Danish meteorological station at Kornok. The climatic optimum of the fjord lies further inland, towards Ilulialik (cf. Longstaff (7)), but the site is protected from the force of winter ice-cap winds by the mountainous high fjaeld inland of it, while the Sadlen block of mountains, and hills to seaward of it, give it partial protection from the sea winds, broken by the wide north arm of the fjord. It does not represent fully the continental character of the Low Arctic regime, being shown to be close to the meeting-place of sea and ice-cap wind systems, both by the botanical evidence—the changes in the orientation of espaliers, the desiccation of the sides of shrub patches and their degree of decumbency and mat-growth, observed up the fjord—and by the presence of a local cloud-region about the Ivisat hills described by O. Nordenskjold (27), and by Dr Church, as characteristic of this situation.

In this subcontinental region we experienced a fairly regular sequence of light morning south-easters, warm and dry, and of afternoon or evening south-westers, cool and moist or showery, though often enjoying a pocket of fine weather when the hills about were clouded. This sequence was interrupted by occasional hot, calm days followed once by thunder in the hills, with 10 hours torrential rain, and once by a violent storm. The precipitation for the year at Kornok was 36·5 cm. in the past averages. In the winter the snow is stated to lie from about October (cf. 6, 9) and to be blown into hollows between ice-bound rock domes. In the summer snow and hail were only experienced at high altitudes. Dew is negligible in the brief night, and evaporation sufficiently great for ponds under 40 cm. in depth, tepid in summer, to dry out partially or entirely under the present cycle of climate. The balance of precipitation and evaporation may become critical on porous soils, especially where little winter snow collects and insolation is direct.

During the $5\frac{1}{2}$ months of the frost-free period temperature rises with great rapidity, and by mid-June only one abnormally late snow-patch could be found in the region. During a representative 18 days' observations in the last week of June and first fortnight of July, air temperatures at 9.30 a.m. were found by E. M. N. to average 10·5° C., with max. 15° C. and min. 7° C., the extremes observed through the day being 19·5 and 5° C., with greatest range in afternoon or evening according to the character of the wind. The "nights" are warm, 3° C. representing an exceptionally cold midnight, and 9° C. observed at dawn. As the Kornok July mean was 8·4° C. it seems that mid-summer temperatures at Isersiutilik in 1928 may have exceeded its average by over 2° C., a difference typical of the great yearly and local variation found throughout the land belt (cf. Petersen (21) and Rosenvinge (51)). After this variable summer, temperatures fall again to their minimum in January, when the Kornok mean was − 10·8° C.

Orographic variation. The climate is considerably modified by physiographic factors, especially by major changes in slope and elevation, and such effects are referred to as orographic variation. Slopes receive the greatest

insolation, and on these the most favoured sites are snow-holding ledges backed by steep rock walls, whose re-radiation of the sun's warmth melts the snow from behind. Thus the normal lapse rate of 0·6° C. per 100 m. (**20**) has a variable significance, and elevations are grouped artificially as follows:

100–300 m. (330–990 ft.): Lower Montane Zone.

300–500 m. (990–1650 ft.): Middle Montane Zone.

500–700 m. (1650–2310 ft.); and higher: Upper Montane Zone.

Rosenvinge (**51**) attributes very great importance to differences in exposure to or protection from the "foehns" in determining the vegetation of slopes in the southern fjord region. How far this applies to the foehn in the highlands of Godthaab Fjord is uncertain, but there is no doubt that it applies to the winter ice-cap winds in general. The only qualification to be made is that blocks of land further from the ice, as the Ivisat high fjaeld referred to later, may suffer less from snow removal to the north-east and certainly feel the force of south-westerly gales from the sea. At lower altitudes the westerly slopes are more protected, however, and carry the more luxuriant vegetation in the central parts of the fjord.

The most important difference between individual blocks of the highlands is that produced by the wind system in which each falls. This is here expressed by the differences in insolation produced, the maritime, and also, as noted, some subcontinental hills, being cloudy, whereas the continental hills appear from their vegetation to enjoy abundant sunshine. Their drier atmosphere was borne out by the wonderful visibility from their summits, whence the ice-cap, with every shadow sharp, appears as an anomaly in the hot sun. Two types are described accordingly:

Cloudy type. Subcontinental high fjaeld of Ivisat and neighbouring blocks, with midsummer snow-patches in upper montane and sometimes in middle montane zone, frequent from 500 m. upwards: characterised by frequency of *Salix herbacea* and various late snow plants: optimum sites inferred to be southerly exposures where the snow melts early, together with south-westerly slopes when sheltered from the sea.

Sunny type. Continental high fjaeld sampled at Ilulialik, with midsummer snow-patches scarce in the upper montane zone and only seen above 800 m.: characterised by frequency of *Cassiope tetragona* and lichens: optimum sites in southerly snow hollows or commonly on the more sheltered westerly slopes.

(2) *Physiographic regimes* (Pl. XVI, phots. 1, 2,
Pl. XX, phot. 9, Pl. XXI, phots. 10, 11).

The retiring ice has left the land-belt scored with a double system of troughs, the main fjord arms meeting its margin at right angles, in a north-easterly direction, while across them lie depressions, lakes or fjord arms, parallel to the ice. The effect of glaciation in this is said to have been the enlarging of pre-Glacial valleys and of diaclases or tectonic weaknesses in the

rock formation (**24**). The double trough system greatly influences the climatic regions in Godthaab Fjord, and the intervening mountain blocks serve to delimit the regions here outlined: the Maritime region seaward of the Sadlen Mountains, the subcontinental region inland of it, about the Kugssuk-Kornok line, and the continental region inland again, beyond the Ivisat uplands (720 m.) and Ivnajuagtok (1200 m.), as far as Ivisartok (1240 m.), upon which the white plain of the ice abuts. The combined width of these belts is about 75 miles.

The rocks between Disco Bay and the Ivigtut region in the south are believed to be a continuous system of pre-Cambrian gneisses and schists with some later intrusions (see (**23**)), and grey gneisses appeared to predominate in the northern arm of Godthaab Fjord. The physiography may therefore here be grouped according to macro-relief in a manner similar to that adopted by O. Nordenskjold (**27**):

Mountain blocks whose summit contours do not show the levelling effect of glaciation. Those in Godthaab Fjord appear from the sea as a snow-crowned sierra, 1000–1600 m. in height, screening the interior, and occupy the southern sector of the fjord system. They have the steep relief of Norwegian fjord country, with talus slopes at their feet, and near the coast small glaciers hang down their northern sides to less than 100 m. above the water.

High fjaeld blocks, typically 300–800 m. in altitude, which have been reduced by the ice towards plateau contours, bearing summit tarns or draining into cirques. Erratic boulders and glaciated pebbles have been left on their summit flats. These highlands, broken by the Ilulialik and Ujaragssuit depressions, occupy most of the northern side of the fjord, inland of Kugssuk.

Low fjaeld. Heavily denuded lowlands, typically under 100 m. in elevation, occupying most of the northern side of the fjord from Kugssuk seawards. Across them low ridges, intercepted transversely by shallow ravines, run out past Isersiutilik, rising again to higher fjaeld of about 300 m. and finally sinking below the sea in a characteristic fence of skerries. Strewn with countless lakes, this country has its replica in southern Sweden.

Silt terraces. Flats of "glacial clays," more or less sandy, sometimes containing water-worn blocks or detritus but often devoid of stones, having been variously deposited by floating ice, lakes and streams at the ice-foot during quaternary submergence of the lowlands (cf. **9**, **10**, **19**). In Godthaab Fjord they form terraces (Pl. XX, phot. 9) about the heads of inlets in the continental region, and appear to fill the valley from Kugssuk head to Taserssuak, forming small plains in a country which is elsewhere a network of irregularities, and attaining to near 100 m. in elevation, with eroded faces 2–30 m. deep. This light grey silt has a high capillarity and lacks the water-retaining powers of a true clay, a Kugssuk sample being found to be a combination of clay with silt and very fine sand. Its sedimentation was found to be accelerated by saline water. This, however, probably only applies to the more clayey examples. On these

are found, especially in exposed places, stoneless clay polygons or "rutemarks," which are peculiarly resistant to colonisation. In the absence of these there are sometimes slight solifluction curves in the soil, across the angle of slope. Drainage is normally by piedmont springs, but locally erosion has carved out deep gullies, for in summer the smooth surface is often hard to cut with a knife, and great run-off must here take place in heavy storms.

Drainage basins. Normal erosion, in Martonne's sense (**26**), has been so slight since the retirement of the ice, that rivers are rare and there is much inward drainage. The lakes are innumerable in parts of the lowlands, and in them lies an untouched field, for biological exploration, with a means of transport more efficient than can be obtained in the hummocks and tangled heath round about. Shallower waterlogged depressions in the region of the lakes are often occupied by peat of the warm "post-Glacial" period referred to later, and such areas are regularly rumpled into systems of close-set turf hummocks by the expansion processes accompanying the freezing of the boggy soil in winter. Such lake and hummock areas are here treated separately from the low fjaeld, though the two are often associated in the same region.

Shoreline. The fjord water is still saline in Kugssuk, though becoming nearly sweet nearer the glaciers at the fjord head, and variable according to tide. The shoreline replicates the types of substratum of low fjaeld and terrace, and its most important characteristics are its varying salinity and the rapid subsidence which is now taking place (see Longstaff (**7**), and Seward (**12**)). Owing to the latter factor the heath turf is being cut back and denuded wherever it comes within reach of ice-thrust and spray, and at this point is found a "neutral zone" with a special vegetation (Pl. XXI, phot. 11). At the fjord head the lower zones of halophytes practically disappear.

Isersiutilik (Pl. XVI, phot. 1). The surveyed ground lay in low fjaeld, including a stretch of shoreline, at the north end of the drainage basin of the largest lake between Godthaab Fjord and Fiskefjord. Typical exposures along the stream and shoreline consisted of granulitic biotite and hornblende-biotite gneisses, fine-grained and hard, and for the most part rich in quartz. Darker bands of diorite gneiss, hornblende schists, pegmatites, and occasional veins of quartz are interbedded. The strike was nearly north and south, and the strata were very varied in compactness and mineral constituents. The main glacial grooves follow the strike, so that across the area parallel rows of rock domes (*roches moutonnées*), and frost-shattered causeways, run between south and south-south-west. Between them the steep-sided tarns lie in chains, being joined by long corridors through the rocks, or linked by strips of detritus across terraced and boulder-strewn flats, or again spreading out into the boggy depressions of small drainage basins. Between these barriers the outward drainage is negligible, but smaller transverse corridors, one system running east to east-north-east, and one south-east, allow an occasional stream to find its way out. These corridors exactly resemble the triple diaclase system

Phot. H. P. H.

Phot. 1. Isersiutilik: view over the Low Fjaeld and the Kugssuk inlet, with Ivisat High Fjaeld in left background: showing undeveloped drainage and sheltered position of Isersiutilik. Lower Montane zone vegetation in foreground with open Mat and some Moss Mat vegetation.
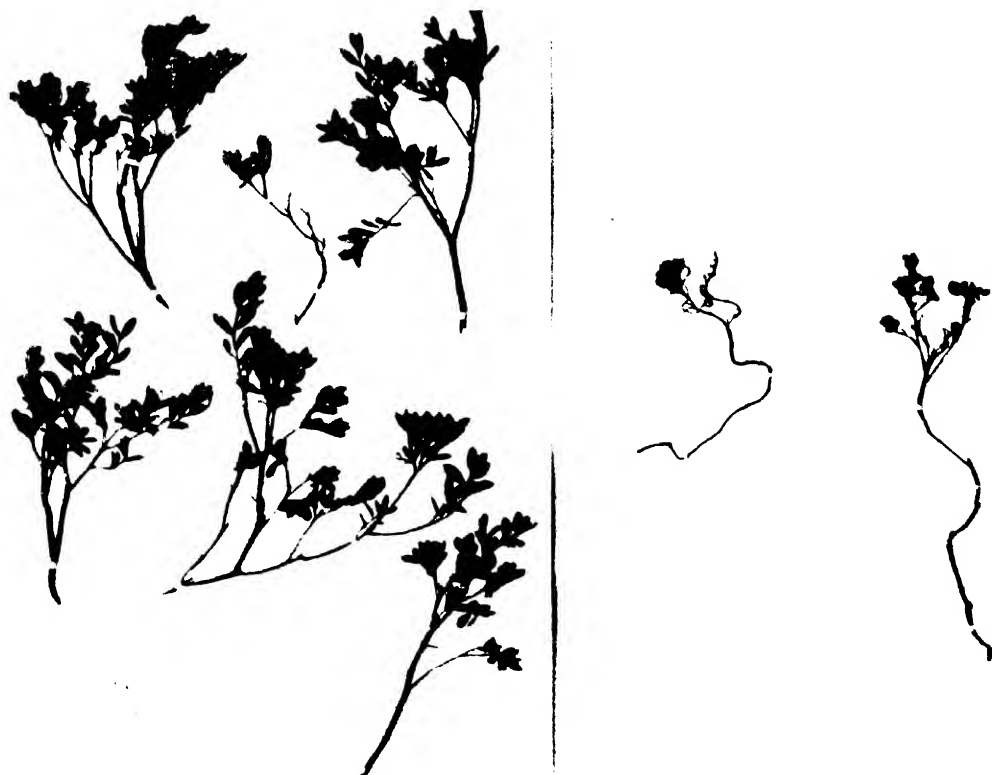
Phot. 2. *Vaccinium* races: Left, *V. uliginosum* f. (no. 283) in flower, from sheltered ground at 550 m. above Huliulik. Right, typical var. *microphyllum* from *Cladina* Mat on the silt terrace at sea level. Collected in fruit the following day.

TRAPNELL—GODTHAAB FJORD

described by Kornerup for the Holstenborg district (**25**). Where they are devoid of soil, as at high altitudes, the angular blocks forming their floor can be seen crushed flat like an ill-metalled road by the weight of ice that once passed along them.

III. VEGETATION.

(1) *Classification* (Pls. XVI–XIX, phots. 2–7).

As has been pointed out on p. 298, under nival conditions, and especially in the Arctic, zonal distribution of large vegetation units of a relatively homogeneous character, appears to be replaced by changing complexes composed of numerous smaller units, themselves variously mixed. The result is generally a lack of dominance and little constancy of association. These features are less pronounced on the relatively uniform surface of a silt terrace or tundra plain than on the fjaeld or rock tundra (cf. **5, 13**). But it is clear that the polyclimax type is general, and its characteristics prevented the working out here of the full classification of Du Rietz (**3, 4**), although the vegetation he deals with in Scandinavia is of similar specific composition. In consequence the following provisional classification is retained, with terminology based on that of Braun-Blanquet and Pavillard (**1**).

The following terms are employed:

Regional type. The layer structure and principal dominant or characteristic species of each layer which predominate through a complex or series of complexes of the same general regime.

Variant. Any sample of a complex taken under a uniform set of external factors; often mixed in character.

Local type. The layer structure and principal characteristic, dominant or differential species which give a common facies to a number of similar variants.

Association. The full specific assemblage found from a number of variants to be characteristically associated with one local type.

The layers used in classification are as follows:

(A) *Ground layer.* Cryptogams and plants less than 10 cm.

(B) *Field layer.* Phanerogams over 10 cm. in normal growth.

(C) *Shrub layer.* Shrubs over 1 metre.

The layer structure is defined in the key below ((1), (2), (3), etc.), in which the local types recognised under different conditions in Godthaab Fjord are under their various classes. In their definition, following the principle of Cajander, primary importance is attached to the ground layer (**2**), which is most subject to the differentiating effects of competition.

(1) *Open vegetation.* Ground layer markedly discontinuous: field layer, where present, chiefly scattered herbs (cf. **54**).

    (*a*) Cryptogams of ground layer most conspicuous.

        Scattered *Solorina crocea* among sparse crusts of *Polytrichum alpinum*, under 2 cm.; sometimes *Bryum* or *Pohlia* spp.; with few phanerogams as *Phippsia algida* or *Cassiope hypnoides* (cf. **41, 42, 65**).   **Solorina–Moss Barren.**

Open *Rhacomitrium hypnoides* or *Rhacomitrium* spp. with sparse *Cetraria* spp., typically *C. hiascens*, and scattered field layer of *Poa glauca*, *Luzula confusa* or *Carex* spp. (cf. **42, 65**).   **Luzula-Moss Barren.**

(*b*) Herbs of field and ground layers most conspicuous.

Scattered flowering plants of polar or high arctic type, chiefly *Papaver nudicaule* with *Saxifraga oppositifolia* or *Draba* spp., with very few cryptogams (cf. **42, 44, 53, 54, 65**).   **Poppy Herb Barren.**

Oxyria reniformis common, typically with *Saxifraga comosa* or spp., *Cardamine bellidifolia* and *Ranunculus pygmaeus*, with some mosses and hepatics.   **Oxyria Herb Barren.**

(2) *Open Mat.* Ground layer sparse but continuous in small or shallow patches; open field layer usually present.

(*a*) Lichen ground layer dominant without subshrub field layer.

Cladonia gracilis, typically var. *elongata*, dominant in a sparse 5 cm. carpet on litter of *Salix herbacea*, with other lichens but few mosses. (Sometimes closed.) (Cf. **39, Fig. 3 b.**)   **Cladonia Mat Barren.**

(*b*) Lichen or mixed ground layer among cushion subshrubs.

Cushions of *Dryas integrifolia* among sparse *Alectoria ochroleuca* or spp., with *Cetraria nivalis* or *Lecanora tartarea* var. *frigida*. Some xerophytic herbs such as *Carex nardina*. (Also closed?) (Cf. **39, 45, 50, 65, 66**.)   **Dryas Mat Barren.**

Cushions of *Diapensia lapponica*, sometimes with *Loiseleuria procumbens*, or with xerophytic herbs, e.g. *Juncus trifidus* or *Luzula* spp., among *Alectoria nigricans* or spp. and *Lecanora*, on *Gymnomitrium coralloides* and small mosses (cf. **4, 51, 57**).   **Diapensia Mat Barren.**

(*c*) Moss ground layer and dwarf shrub field layer.

Cassiope tetragona dominant in a rather sparse field layer with or without associates of the *Dryas* type among mosses, e.g. *Dicranum* and *Polytrichum* spp. in small quantity. (Also closed?) (Cf. **39, 45, 49, 66**.)   **Cassiope Mat Barren.**

(3) *Lichen Mat.* Ground layer, with lichens predominating, continuous, hiding stones or forming a dense turf or carpet 2 cm. and upwards in depth; field layer absent or discontinuous or in small patches (cf. **51**).

(*a*) Ground layer shallow (2 to 5 cm. approx.), with white Cladinae absent or sparsely scattered.

Cetraria hiascens dominant, usually with some *Salix herbacea* and few *Dicranum* and *Cladonia* spp., scattered herbs, e.g. *Arenaria Groenlandica*, and occasionally *Loiseleuria procumbens* or *Empetrum hermaphroditum* (cf. **4, 55**).   **Cetraria Mat.**

Alectoria ochroleuca dominant with *Sphaerophorum melanocarpus* and other lichens, usually concealing crust-mosses of (*b*), with *Vaccinium uliginosum* var. *microphyllum* abundant, or *Rhododendron lapponicum*, and scattered xerophytic herbs (cf. **4, 54, 55**).   **Alectoria Mat.**

(*b*) Ground layer deeper (5–15 cm.), with white Cladinae numerous and conspicuous.

Cetraria nivalis plentiful, with numerous mixed *Cladonia* spp. in a low or loose ground layer, with *Pohlia nutans* and *Polytrichum juniperinum*, among *Betula nana*, often decumbent. *Vaccinium microphyllum*, *Ledum decumbens*, and herbs as *Hierochloe alpina* associated (cf. **4, 37, 45, 48, 49, 59**) (Pl. XVII, phot. 3).   **Birch-Lichen Mat.**

Cladinae, typically *C. mitis* and *C. alpestris*, interwoven with *Stereocaulon paschale* in dense tall carpet. Dwarf shrubs, typically *Betula nana*, and grasses, etc., widely spaced when present, and mosses of above entirely restricted to cracks (cf. **4, 51, 57, 59, 63, 64, 67, 70**).   **Cladina Mat.**

(4) *Moss Mat.* Ground layer with mosses predominating, structure as last. Field layer absent or discontinuous or in small patches (cf. **51**).

(*a*) Field layer of dwarf shrubs absent or inconspicuous.

Salix herbacea abundant, often with *Cassiope hypnoides*, in a 2–5 cm. moss mat,

Phot. 3. Exposed Lichen Mat: Birch-Lichen Mat on talus soil with *Betula nana* in adpressed crescents due to wind driving of snow. *Cetraria nivalis* dominant in shallow Lichen Mat between the shrubs, exposure being too great for *Cladina*. Partly desiccated *Ledum groenlandicum* among birch in foreground.

Phot. 4. Herb Mat: *Archangelica officinalis* skeletons and leaves standing above tall Cyperaceae and grasses in moist situation at Kugssuk Head. Willow scrub occupies site of snow drift at base of rocks, benefiting from southerly aspect and probably from re-radiated warmth. *Alnus incana* close to waterfall.

chiefly *Dicranum molle*, often with *Drepanocladus uncinatus* and Hepaticae. (Sometimes Open Mat.) (Cf. **39, 48, 51, 60, 65, 68, 69**.) **Salix-Moss Mat.**

Rhacomitrium hypnoides dominant, without or submerging dwarf shrubs of next, often with *Dicranum elongatum* and *Polytrichum strictum* var. *alpestre* and associated lichens, in a 5–10 cm. mat, with scattered herbs, e.g. *Luzula* spp. (cf. **4, 37, 51, 60, 61, 65, 66, 69**). **Rhacomitrium-Moss Mat.**

(*b*) Field layer of dwarf shrubs conspicuous or in patches.

Empetrum hermaphroditum dominant with *Vaccinium uliginosum* f. and occasional *Bryanthus coeruleus* in ground layer of *Dicranum* spp., often with *Ptilidium ciliare*, *Polytrichum strictum* var. and other bryophyta and lichens of *Nephromium* group (cf. **4, 39, 51, 60, 66, 69, 72**). **Empetrum-Moss Mat.**

(5) *Patchwork Mat*. Field layer of dwarf shrubs discontinuous in large patches, with lichens and mosses equally conspicuous, intermingled or in patches.

Empetrum hermaphroditum and *Betula nana* co-dominant shrubs with patches of *Cladonia alpestris*. *Drepanocladus uncinatus* commoner than other mosses (*Dicranum* spp. and *Polytrichum* spp.); *Cladonia coccifera*, etc., and scattered herbs, e.g. *Carex rigida* var. *concolor*, associated (cf. **4, 48, 51, 64**). **Empetrum-Birch Mat.**

(6) *Heath Mat*. Field layer of dwarf shrubs continuous, hiding ground layer, or its large patches clearly dominant (cf. **50**).

Vaccinium uliginosum f. dominant, with *Carex rigida* var. *concolor* and occasional *Salix chloroclados* or *Betula nana*, with ground layer of *Drepanocladus uncinatus* or other hypnoid mosses (cf. **4, 51, 60**) (Pl. XXI, phot. 10). **Vaccinium Mat.**

Ledum Groenlandicum dominant or co-dominant with *Betula nana* or the two in alternes, with concealed ground layer of *Hypnum schreberi*, and *Drepanocladus uncinatus* associated, and locally *Coptis trifoliata* or *Hieracium lividorubens*. *Calamagrostis Langsdorffii* frequent. **Ledum-Birch Mat.**

(7) *Herb Mat*. Herbs dominant in a close ground layer or grass field layer.

Sibbaldia procumbens common; *Polygonum viviparum*, *Lycopodium alpinum*, *Gnaphalium supinum* and other associates, with few grasses, e.g. *Trisetum spicatum* or *Phleum alpinum* (cf. **39**). **Dwarf Herb Mat.**

Field layer of *Calamagrostis Langsdorffii* and *Deschampsia flexuosa* dominant, with associated *Poa alpigena* and herbs, e.g. *Luzula* and *Carex* spp., *Pirola minor*, etc. (cf. **37, 39, 49, 51, 53, 54, 59, 70**). **Grass Mat.**

(8) *Scrub*. Shrub layer continuous, hiding field layer.

Salix glauca (×*chloroclados*) forming a 1–2 m. scrub with associated *Alnus incana*. Field layer typically open grasses with ferns, *Potentilla maculata*, etc. Ground layer typically *Brachythecium* spp. (cf. **37, 39, 48, 51, 53, 54, 70**). **Willow Scrub.**

One example of pure alder scrub was also seen in a silted gorge north of Ilulialik, and *Betula nana* often forms small patches approaching the scrub category, bushes at Isersiutilik once being found approaching 1·5 m. in height.

Types such as Empetrum-Birch Mat overlap others in specific composition though not in facies: they have to be retained because these less differentiated types usually occupy the greatest area. These and other types have been chosen as far as possible to agree with those of other authors, in particular Du Rietz (Scandinavia), Hansen (Iceland), Rosenvinge (South Greenland), and Summerhayes and Elton (Spitsbergen), as indicated by the attached reference numbers.

In some cases taxonomic problems are involved; and among these the following should be noted:

Empetrum hermaphroditum. Described and investigated by Hagerup (**31**): a tetraploid cell giant with palisade cells, and especially intercellular spaces, much larger than those of the boreal *E. nigrum*, and replacing it in the Greenland sector of the Arctic: all West Greenland material examined belongs to this species.

Ledum groenlandicum. Investigated by M. P. and A. E. Porsild (**49**): synonymous with the *L. latifolium* of the boreal American coniferous forests, and of a corresponding range to that of the *L. palustre* races of the boreal Eurasian coniferous forests: closely allied to the American arctic *L. decumbens*, with apparently intermediate forms in Godthaab Fjord.

Vaccinium uliginosum. A polymorphic species investigated by Petersen (**34**). From West Greenland material examined only one example of the main species was found, from the extreme south: the var. *microphyllum* is common through the High Arctic and more continental Low Arctic habitats; fruiting early and abundantly (cf. **49**): the var. *pubescens* as figured by Porsild (**48**) was not seen in Godthaab Fjord, but was replaced by a narrow-leaved pubescent plant, like it, fruiting poorly and late and occupying the more sheltered sites. This form or variety appeared to have a low Arctic distribution in Greenland and is also found in Europe. Intermediates between it and var. *microphyllum* appeared to be frequent. It answers to Hornemann's original figure of var. *pubescens*, but this was questioned by Lange (**32**), and further investigation is needed (Specimen 283 in the Kew Herbarium) (Pl. XVI, phot. 2).

Salix glauca. All specimens collected under this head, covering a great range of variation, were returned as hybrids with *S. chloroclados* by Dr Floderus who has investigated the group (**30**). Type *S. glauca* would appear to be practically lost in Godthaab Fjord upon this interpretation, and the Greenland type separated by Schneider (**36**) as *S. anamesa* to be contaminated stock generally. The variations found in the plants with *glauca* factors dominant are treated by Porsild as including constant races of *S. glauca.* Certainly in Godthaab Fjord there appeared to be recurrent types selected by different habitats, and of these the following require note:

GLAUCA TYPE:

Scrub Willows. The nearest approach to *Salix glauca* as ordinarily understood, generally 1–2 m. high. Normally silky, but patches of glabrescent plants are found (155).

Heath Willows. Often of the last type, but very variable: an erect shrub with silky leaves four times as long as broad, recurs on dry ground throughout the fjord, typically in Birch-Lichen Mat (109 a).

Plateau Willows. Diminutive, creeping, narrow-leaved plants of high altitudes (294).

Intermediate, or approaching *S. chloroclados*:

Knoll Willows. Small, creeping plants with broadly ovate-lanceolate leaves, glabrescent on the upper surface: on dry, rocky elevations, typically in *Alectoria* variants and in the Lower Montane Zone (111).

CHLOROCLADOS TYPE:

Bog Willows. Predominantly or exclusively pure *S. chloroclados* (an American Arctic species of undrained ground, of creeping habit).

These observations are in partial agreement with Floderus, who states that *glauca* hybrids predominate, occupying dry and elevated situations, while *chloroclados* hybrids occur in moist places in the lowlands and rarely in the mountains (**30**). But *chloroclados* types (cf. 413) ascend into the Middle Montane Zone on the Ivisat Block, and they or the type are abundant on the Godthaab coast, both in cloudy regimes.

The figures refer to typical specimens in the expedition's collection in the Kew Herbarium.

Polymorphic species are common in the plant populations, and it is probable that in some, especially in the *Vaccinium* forms cited, there are present a series of more or less plastic ecotypes, as shown by Turesson in the case of the *Campanula rotundifolia-Gieseckiana* population in northern Europe (**14**). Porsild (**49**) and Turesson agree in finding that the more northern forms or varieties are the early-maturing ones, as here noted in the two extreme forms of the *Vaccinium* population.

(2) *Climatic types.*

The distribution of regional climatic types appears to be best conceived as a series of elongated, much interrupted belts, roughly parallel to the ice-margin, but tending to commence in the more sheltered interior in the north and to terminate in the south nearer the coast. This qualification would not apply to those elements characterised by *Cassiope tetragona* (**66**), *Alectoria ochroleuca* (**55**), or dominant species of *Cladina* Mat (**51, 59**), which appear from the authors cited to be intolerant of the fog of the maritime conditions.

Numerous cases of discontinuous distribution of species, particularly American Ericaceae and species held to have immigrated from America in the warm post-Glacial period, complicate the definition of types, but may be resolved by further exploration. The most remarkable change is the replacement of *Betula nana* by *B. glandulosa* in the south (**33**). The true boreal immigrants are now mostly isolated in favoured situations, notably *Betula odorata* ("var. *tortuosa*") in the south, though this appears, from pollen analyses made by Dr K. Jessen on peat samples of the expedition, to have been found about the interior of Godthaab Fjord in the warmer period. Upon the basis of the more widely distributed plants the main climatic types are outlined below for the west coast, with special attention to those represented in Godthaab Fjord. Their subdivisions, the physiographic types, as recognised in the fjord, are given subsequently.

It will be seen that each of the major regimes has one or more species characteristically associated with it in abundance and one or more dominant local types. It must not, however, be presumed from this that uniform types necessarily prevail over large areas. Most varied combinations of species are found, and the dominant local types are sometimes only the expression of the average combination seen, while scarce combinations are generally omitted.

Polar climate (North Greenland to Baffin Bay coast?). Open herbaceous vegetation (fjaeldmark of Warming (**54**)) with *Papaver nudicaule, Luzula confusa, Oxyria reniformis, Cardamine bellidifolia, Dryas* and *Saxifraga* spp., etc. typical. *Rhacomitrium hypnoides* the chief moss, with *Polytrichum alpinum, Bryum* and *Pohlia* spp., etc. Lichens undescribed, but *Alectoria* and *Cetraria* communities found in Ellesmereland by Simmons (see (**56**)). See Ostenfeld on collections of Wulff (**44**) and Freuchen (**42**), and general account (**43**), and cf. Summerhayes and Elton on Barren and *Dryas* Zones of the Spitsbergen Archipelago (**66**).

High Arctic climate (inland of Baffin Bay to north Disco Island?). Probably Open Mats of *Cassiope tetragona, Dryas integrifolia, Rhododendron lapponicum,* etc., with *Vaccinium uliginosum* var. *microphyllum* and locally *Empetrum, Betula* and *Ledum decumbens* entering in more favoured spots. Scattered xerophytic *Luzula, Carex* and *Poa* spp., with other grasses, e.g. *Trisetum spicatum* or inland, *Hierochloe alpina.* Other herbs, e.g. *Draba* and *Cerastium* spp.,

Oxyria, *Papaver*, etc., being restricted to unfavourable places near the coast. Mosses, locally dominant on the coast, *Rhacomitrium hypnoides*, *Polytrichum*, *Dicranum*, *Conostomum* and *Bryum* spp., etc. Lichens apparently *Alectoria*, *Cetraria* and some *Cladonia* spp., with *Solorina crocea* near the coast. Both *Dryas*, and typically *Cassiope*, are described as forming "heaths," but in transitional conditions, between lat. 72° 31′ N. and the south of Disco and neighbouring coast, this *Cassiope* type begins to give way to low arctic variants such as *Empetrum*-Birch Mat, and in drier parts, Birch-Lichen Mat, and to this transition region the data obtained by Holttum refer (**39**). See Porsild (**46, 47, 48, 49**), Brown (**37**), Taylor (**52**), Kruuse (**40**) and Lynge (**41**), and cf. Summerhayes and Elton (**66**) on *Cassiope* and Inner Fjord Zones of the Spitsbergen archipelago.

Maritime Arctic climate (outer portions of the land belt from Farewell to the Holstenborg region). Moss Mat, with Open Mat close to skerries. *Empetrum hermaphroditum* and *Salix herbacea* chief dwarf shrubs, with *Vaccinium uliginosum* f. or var. frequently associated and sometimes abundant. *Loiseleuria procumbens* and *Bryanthus coeruleus* less common, and sometimes scattered hybrid willows of the *chloroclados* group. Grasses plentiful and varied; at Godthaab *Deschampsia flexuosa* and *Festuca ovina* var. *supina* f. *vivipara* the most plentiful, but other species as *Poa* and *Agrostis* spp. or *Trisetum spicatum* may figure elsewhere. The various species of Herb Mat seem to be little affected by maritime conditions, *Taraxacum croceum* being conspicuous in this respect, while *Calamagrostis*, *Luzula* and *Carex* spp. were also present, and *Polygonum viviparum* is typically abundant. Typical mosses are *Rhacomitrium hypnoides*, *Dicranum molle*, *D. elongatum*, *Conostomum tetragonum*, etc., and of the lichens, which, contrary to the opinion of Warming (**53**), were conspicuously few, *Cetraria hiascens*, *Cladonia gracilis*, *Parmelia pubescens* (?), *Solorina crocea* and possibly other less frequent Peltigeraceae, seem typical. The frequency of herbs, however does not seem so great as described by Hadwen and Palmer (**59**) for the Alaska coast, nor the frequency of *Vaccinium uliginosum* f. as great as described by Hansen (**60**) for Iceland.

Owing to lack of insolation, assimilation and transpiration must alike be retarded in the critical periods of growth and reproduction. *Empetrum*, though plentiful and strikingly green in foliage, had little fruit at Godthaab and that still green, at the beginning of August, 1928, while no *Vaccinium* fruit was seen then and the stunted plants were often only 5 cm. in height. Late-flowering southern types suffered most, *Chamaenerium angustifolium* being reduced to 5 cm. in height, with buds scarcely showing on the date referred to. Even the northern *C. latifolium* was reduced to 15 cm. in height, as in the subcontinental upper montane zone. Not only was there a scarcity of heliophilous lichens, such as the *Cladonia* spp. to which Wiesner attributes high light requirements, but his claim that the range of illumination tolerated diminishes as plants approach their northern limit was borne out in that

Betula nana was in the state of reduced branching described by him as symptomatic (**15**). Only a few trailing stems of it were seen, while *Juniperus communis* var. *nana* and other heliophilous shrubs of the inner fjord were rare or absent. But grasses were common, as noted also by Rosenvinge (**51**) in the south, and the hemicryptophyte composition of the vegetation differed little from that of the inner fjord except for the absence of some continental species such as *Hierochloe alpina*. The late snow is probably as important as the dull and chilly summer, and plants characteristic of these and "Schnee-tälchen" conditions, such as *Bryanthus coeruleus, Salix herbacea, Cassiope hypnoides, Gnaphalium supinum* and *Sibbaldia procumbens*, were numerous in species and unaffected in reproduction.

Variants were listed with avoidance of the disturbed ground about the settlement, which has an untypical, often nitrophilous, vegetation with luxuriant *Poa alpigena* var. *domestica*. Results agreed closely with those of Rosenvinge (**51**) on the south coast, and data from the two sources are here combined, giving the following distribution of local types[1]:

Open.	Oxyria Herb Barren: traces in snow gullies, G.	
	Luzula Moss Barren: traces, to frequent, on outer coast, G.	
Open Mat.	Diapensia Mat Barren: patches of this type, G, J?	
Moss Mat.	Rhacomitrium Moss Mat: characteristic of coastlands, J.	
	Salix-Moss Mat: common on coastlands, G, but also in J.	
	Empetrum-Moss Mat: typically dominant, G, J.	
Patchwork Mat.	Empetrum-Birch Mat: inland only, G.	
Heath Mat.	Vaccinium Mat: stunted, in moory places, G.	
Herb Mat.	Dwarf Herb-Grass Mat: scattered pockets, G.	

In this and the following examples, H refers to the northern and Holstenborg sector of the land belt, north of the Sukkertoppen ice arm, G to the Godthaab sector south of it, and J to the Julianshaab sector south of the Frederickshaab ice arm, where Atlantic depressions have most effect.

In general the rocky and desolate character of these coastlands is not concealed by the low green patches of vegetation or the shallow soil, through which naked talus often shows. The general type is that of north exposures and late snow sites of the lowlands of the subcontinental region of Godthaab Fjord, and of the Middle and Lower Montane Zones of its highlands. See Rosenvinge (**51**), and cf. Summerhayes and Elton on Bear Island (**65**), Hansen on Iceland (**60**), and Watson on the arctic-alpine vegetation of Scottish mountain tops (**69**).

Low Arctic climate (typical variants are first referred to by Porsild in 72° 30′ N., but probably do not become dominant till south of Disco Bay, extending thence through the interior to the south, where they begin to

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[1] The variants noted do not cover deflated, open Empetrum-Moss and Cetraria types, the former seen on southerly exposures, and the latter with Luzula-Moss Barren on northerly exposures. Cetraria Mat is to be looked for in less exposed situations, and also Cladonia Mat Barren. Cf. figure in **Holttum** (**39**) of *Cladonia gracilis* Mat on *Salix herbacea*.

assume a boreal character in subcontinental valleys). Lichen Mat, with Heath Mat in more humid or subcontinental situations, with pockets of Herb Mat and Scrub scattered throughout, but only assuming importance in the boreal transition localities.

In the more continental part of the Godthaab sector *Betula nana* is the dominant shrub, with *Vaccinium uliginosum* var. *microphyllum*, and *Ledum decumbens* among less plentiful associates: *Empetrum hermaphroditum* and *Ledum groenlandicum* are common, but favour westerly slopes, while *Empetrum* is thrust into less favourable situations, close to the fjord margin. *Hierochloe alpina* is the typical grass, but *Deschampsia flexuosa* and *Calamagrostis Langs-dorffii* are common, chiefly in association with scrub, while in addition to numerous herbs in such situations, *Chamaenerium angustifolium* and *Lyco-podium annotinum* var. *pungens* are generally frequent. Mosses of the sub-continental region, such as *Drepanocladus uncinatus* or *Hypnum Schreberi*, are present, but *Polytrichum juniperinum* and *Pohlia nutans* seem characteristic. They are associated with abundant lichens (*Cladonia* spp. and *Cetraria nivalis*), especially those of Cladina Mat, in which *Cladonia mitis* and *Stereocaulon paschale* are here dominant. In the foehn regime of the Julianshaab sector the *Empetrum*, and possibly the Ledums, disappear, the *Betula* species change and the lichens of Cladina Mat become more extensively dominant.

With the high insolation vital processes are rapid. *Empetrum* had ripe fruit in mid-June, a month earlier than the same species in Britain. *Vaccinium uliginosum* var. *microphyllum* and even *Juniperus communis* var. *nana*, had ripe fruit in the first week of July, tall *Chamaenerium angustifolium* flowered then with other late species, and *Hierochloe alpina* had already shed its seeds. But the sun and dry winds make high demands on transpiration. *Empetrum* leaves turn yellow to brown shortly below the growing point, and the *Vac-cinium* and other plants develop anthocyanin pigments. Most conspicuous are the effects of a brief and shallow snow cover, *Diapensia*, *Empetrum*, Scrub Willows and Juniper alike showing dead wood or desiccated shoots, while the late snow plants of the coast were absent, or rare. In their place, invading even Ledum-Birch Mat and Willow Scrub of derelict types, are the lichens, the sun-loving species of Wiesner (**15**) and the snow-free species of Rosenvinge (**51**) and Du Rietz (**57**).

In this glacial steppe the bogs are narrowed to a fringe about evaporated pools, and even xerophytes such as *Diapensia* can enter them. The birches are often matted down to 15 cm. crescents before the easterlies, with sparse *Empetrum* retiring under their lee, while beneath the crumbly lichen carpet the leaves of former shoots lie for years without mouldering. Alders and scrub willows may be reduced to 70 cm., and even plants of Alectoria Mat, as the hardy *Pirola grandiflora*, can be found under their shade in situations close to the ice. But the impression of aridity conveyed by the grey and yellow lichens and the dull green of sclerophyllous shrubs is in marked contrast to

Phot. W. G. H. D. C.

Phot. 5. Willow Scrub: interior of 1 m. scrub at Isersiutilik, the undergrowth of *Calamagrostis Langsdorffii* and associated *Alchemilla filicaulis* and *Archangelica officinalis*, characteristic of the moister subcontinental type.

TRAPNELL—Godthaab Fjord

the luxuriance of the snow drift of the cliff foot, of watercourses, and of recessed valleys. Here the birch espaliers attain $1\frac{1}{2}$–2 m. in diameter or are replaced by 1 m. "scrub" patches and the scrub willows, in small coppices in tall grass, frequently exceed 2 m. in height. In a river gorge north of Ilulialik the scrub was practically continuous along the screes. *Alnus incana* is commonly associated, and specimens still exceed 2 m. at 100 m. altitude, while a 1·5 m. specimen was found even at 200 m. At Ilulialik the scrub willows, with the *Archangelica officinalis* of the streamlets, and other associates, ascend steep south-westerly ledges into the Middle Montane Zone, where the last scrub pockets disappear. But close to the ice, at Majuala, the scrub and its associates, of the dry moss and fern type, appeared to cease in the Lower Montane Zone, and the general level of luxuriance falls off again to the wind-swept steppe type. In general the "patchwork" type of the subcontinental region is replaced by denser growth of shrubs with more Heath Willows. The local types of this regime, and their inferred distribution, are as follows:

Open Mat.	Diapensia Mat Barren: traces on denuded exposures, G, (J?).
Moss Mat.	Rhacomitrium-Moss Mat: rare, on westerly exposures, G.
Lichen Mat.	Alectoria Mat: traces, with first, and easterly exposures, G.
	Birch-Lichen Mat: typically dominant, G; with last, H?
	Cladina Mat: locally extensive, G; generally so, J?
Patchwork Mat.	Empetrum-Birch Mat: westerly slopes, general but mixed, G, (H?).
Heath Mat.	Ledum-Birch Mat: south-westerly lees, general, G.
Herb Mat.	Grass Mat: frequent pockets in favoured sites, G, J?
Scrub.	Willow Scrub: frequent coppices in favoured sites, G, (J?) (Pl. XVIII, phot. 5).

The subcontinental part of the Godthaab sector differs somewhat from the type described, as will be seen from the account of it at Isersiutilik on pp. 318–20. But there are greater changes in the Julianshaab sector (51). Towards the coast *Betula glandulosa* and *Vaccinium uliginosum* f. or var. are co-dominant, and *Salix glauca* or hybrids common, in the heath. Willow scrub increases in extent, especially inland, while grass mat occupies the less sheltered slopes. In the heart of this sector, in sheltered glens, these begin to give way to small stands of *Betula odorata* of coppice habit, with *Anthoxanthum odoratum* and *Hylocomium* spp. added to the varied herb and moss associates. This is the latest relict of a past vegetation of a more boreal character, the path of whose retirement is marked by the willow pockets extending north for 10° of latitude to the upper limit of the Low Arctic complex. The heath is close by, and nearer the ice typical lichen variants are extensive or dominant in it. Here, as in the Godthaab sector, they have invaded heath and scrub alike. Finally there are still found in this southernmost part "fjaeldmark" or Mat Barrens of *Dryas* or *Diapensia* types in the exposed situations. Thus the appearance of the first birch stands of *B. odorata* does not necessarily stamp the vegetation south of lat. 62 as a distinct type as Holttum implies (39), even with the more extensive grass and scrub. Rather it should be said that the changing proportions of the local types of the Low Arctic complex of vegetation here reach

the point at which they link on with high Boreal vegetation. Spruce (see Holttum) will just grow at this point, and the Heath Mat and Lichen Mat are about to make the transition to heath-birchwood and Cladina-pinewood by which they seem to pass over into spruce forest in subcontinental and continental Lapland. The complex in this southern region has been fully described by Rosenvinge (**51**). Inferences regarding other parts are drawn from notes of Porsild (**48, 50**) and from photographs. For allied vegetation in Lapland reference should be made to Du Rietz (**4**), Ruggles Gates (**64**), and others.

<div style="text-align:center">(3) Isersiutilik (Pl. XIX, phots. 6 and 7).</div>

The area surveyed by the expedition and the country round it falls under the general head of Low Arctic vegetation, but differs from its most typical form in that Isersiutilik represents the subcontinental part of the Godthaab sector.

The subcontinental part of the Julianshaab sector has already been re-ferred to. Its most typical vegetation is of the patchwork type in which mosses and lichens are equally balanced in the ground layer. Of the dwarf shrubs *Empetrum hermaphroditum* and *Betula nana* are here co-dominant, with *Ledum Groenlandicum* locally abundant, but generally arising in the centre of birch patches owing to greater snow protection: *Vaccinium uliginosum* f. is abundant in the moister parts, and the *Vaccinium* forms taken collectively are very widely distributed, and may be reckoned as second only to the *Betula* and *Empetrum* in importance. Heath Willows are scattered and Scrub Willows only locally plentiful, while generally only isolated individuals exceed a metre in height. Of scattered herbs *Polygonum viviparum*, *Carex rigida* var. *concolor*, *Deschampsia flexuosa*, *Calamagrostis Langsdorffii* and *Luzula spicata* are com-monest.

The cryptogams, very numerous in species, form a close mat of competing mosses and lichens occupying the interstices between the dwarf shrub patches, covering an area equal to them and sometimes more extensive. *Drepanocladus uncinatus* and *Dicranum* spp. are the dominant mosses, with *Polytrichum strictum*, its var. *alpestre*, and *P. juniperinum* common in considerably smaller quantities. The smaller mosses, such as *Conostomum tetragonum*, have been ousted by competition except from the poorer heath of exposures, and in the *Dicranum* cushions are found instead numerous small hepatics, *Lophozia ventricosa* and spp., with *Ptilidium ciliare* frequently growing on top. Of the many conspicuous lichens *Cladonia alpestris* is the most abundant, other out-standing species being *Stereocaulon paschale*, co-dominant with it in the small examples of Cladina Mat found here, *Cladonia mitis*, *C. furcata* and var. *spinosa*, while *Cladonia* spp. with simple podetia, such as *C. coccifera*, are common but do not form the same close mats: *Cetraria* spp. are common, and especially the mat-forming *C. hiascens*.

Phot. W. G. H. D. C.

Phot. 6. Patchwork Mat: *Empetrum Betula* Mat variant, showing in left foreground *Empetrum hermaphroditum*, centre and right *Betula nana*, and scattered white patches of *Cladonia alpestris*. Further back dark patches of *Cetraria hiascens* mark local tendencies towards *Cetraria* Mat. *Vaccinium uliginosum* f. becomes more frequent in the corridor left background. Typical Isersiutilik Low Fjaeld.

Phot. F. M. N.

Phot. 7. Sheltered Lichen Mat: variant of Birch-Lichen Mat, but with tendency to *Cladina* Mat, of which small patch appears in foreground. *Betula nana* in erect bushes at 3–4 yard intervals. Both vegetation and split erratic boulder show tendency towards continental conditions. Phot. inland of Isersiutilik.

TRAPNELL—GODTHAAB FJORD

The patchwork type is the most extensive over the typical low fjaeld, but on dry plains further in from the fjord, among scattered erratic boulders, more continental variants begin to appear, possibly encouraged by greater warmth as well as drought. An extensive area was reported by E. M. N., distinguished by large, erect brushes of *Betula nana*, 2–3 ft. high, usually spaced at 3 to 4 yard intervals, the interstices occupied by lichens of the Cladina Mat group. The other shrubs, and notably *Empetrum*, tended to grow under the birch bushes, and not in patches alongside as in the patchwork type. In similar country in the western Ivisat foothills the birches form espaliers of great size but are adpressed to the rocks owing to greater exposure, and the plentiful *Cetraria nivalis* among the *Cladonia* spp. stamps these variants as of the Birch-Lichen Mat type. In them *Empetrum* becomes scarce, *Vaccinium uliginosum* f. gives place to abundant var. *microphyllum* and *Ledum decumbens* replaces *L. Groenlandicum*. The herbs of the patchwork type diminish in numbers, but *Lycopodium annotinum* var. *pungens*, *Hierochloe alpina*, and even *Chamaenerium angustifolium* become frequent. Where *Empetrum* does come into the open, it is of habit straggling with much dead wood, and herb and scrub vegetation are very restricted about wet places, the dry *Deschampsia-Polypodium-Brachythecium* type of ground layer replacing the moister *Calamagrostis-Archangelica-Sphagnum squarrosum* type which predominated at Isersiutilik.

Greater insolation, with higher temperatures and greater saturation deficit than on the coast must lead to greater transpiration losses and more rapid assimilation, but, compared with the typical interior region, reproduction is still handicapped for southern species. For example, *Juniperus communis* var. *nana* scarcely sets fruit except on sunny cliff ledges, helped here, no doubt, by the re-radiation referred to under the head of Orographic Variation. Reproduction in general is a week to a fortnight behind that of the continental valleys, but three weeks to a month ahead of the coastlands, though a generalisation of this sort must necessarily vary according to the proportion of susceptible and late-flowering southern types and of early flowering northern types observed. On our arrival in mid-June *Empetrum* was already showing numerous berries, the lower ones already black, though those nearer the growing point were still mostly small and green. From this time onwards they turned black in rapid sequence, this "continuous" fructification, in contrast to the "simultaneous" fructification of the Vacciniums being of the greatest importance to the bird population. Other plants setting fruit on this date were *Bryanthus coeruleus*, *Pedicularis flammea* and the heath and knoll willows (*glauca* hybrids), the *chloroclados* group of willows being somewhat later and thus having the same reproduction season as at Godthaab. The air was pungent with *Ledum Groenlandicum* in full blossom, and the Vacciniums, especially var. *microphyllum*, were flowering. During the ensuing month *Vaccinium uliginosum* var. *microphyllum* came suddenly into full fruit, the grey

willows split their follicles and *Pedicularis* capsules became brown and ripe. The ripening of *Vaccinium uliginosum* var. *microphyllum* and of the few fruits of *Juniperus communis* var. *nana*, together with the falling of *Hierochloe* seeds, took place at least a week later than in the continental region, while the flowering of *Chamaenerium angustifolium* and the ripening of the sparser fruit of *Vaccinium uliginosum* f. was deferred to the end of July. It is especially important to stress the ecotype concerned in making phenological comparisons of this sort: for example the races of *Campanula* grouped here under the name of *C. Gieseckiana* flowered in late June and early July in the interior of Godthaab Fjord, whereas the scarcely distinguishable races grouped under *C. rotundifolia* in England flower from July to August, despite their more favourable climate. One of the chief qualifications of the Arctic ecotype is its ability to maintain a continuous and rapid cycle of reproduction before the freezing temperatures and semi-darkness of winter reduce it once more to complete dormancy.

Probably owing to greater humidity and snow cover than in the continental region the growth of plants here is considerable. Among the woody plants, *Betula nana* for example not only commonly exceeded half a metre, and sometimes, in sheltered hollows, a metre, in height, but it grew with a more open and erect habit. It is true that in the continental region broad espaliers were found on the ground with aerial stems 2 m. long, but these had been able to send out adventitious roots from the branches into the accumulated litter beneath them. The erect scrub growth of the birch was only common in the subcontinental region, and trunks were here measured of 13 and even 16 cm. circumference. The root development of these dwarf shrubs is enormous, especially that of the birch, whose taproot commonly exceeds 2 m. in length, but also those of *Ledum Groenlandicum* and *Vaccinium uliginosum* f., and to a lesser extent of *Empetrum*. The roots are forced to assume a horizontal position owing to the shallow soil of the Low Fjaeld and the dependence of the mycorrhiza on humus, so that root-competition greatly accentuates the tendency to the "patchwork" formation at Isersiutilik. In contrast to the dwarf shrubs, however, the grey willows and the rare alders of this region seldom exceed 1½ m. Moisture-loving hemicryptophytes grow to a great height, Gramineae and Cyperaceae sometimes exceeding half a metre in luxuriant hollows, while *Archangelica* in this situation is 1 to 2 m., and in one case over 2 m., in height (Pl. XVII, phot. 4).

The distribution of local types is as follows:

Open Mat.	Diapensia Mat Barren: exposed knolls and cols open to the north east. Limited; generally deflation sites.
Moss Mat.	Rhacomitrium-Moss Mat: rock domes and exposed knolls, especially with westerly aspect. Small patches.
	Salix-Moss Mat: late snow hollows; small patches, and limited except in exposed parts.
	Empetrum-Moss Mat: lower northerly slopes, and close to fjord. Limited elsewhere.

Lichen Mat.	Alectoria Mat: exposed knolls, especially with easterly aspect and on talus soil. Limited.
	Cetraria Mat: limited on rather exposed northerly slopes, and as small patches in the lower heath.
	Birch-Lichen Mat: dry or rather exposed flats, especially on talus soil. Only locally extensive (Pl. XIX, phot. 7).
	Cladina Mat: dry, sunny slopes and especially corridor crowns, limited or patches.
Patchwork Mat.	Empetrum-Birch Mat: the dominant type on level ground and generally extensive (Pl. XIX, phot. 6).
Heath Mat:	Vaccinium Mat: moist corridor floors, especially in sheltered situations. Limited.
	Ledum-Birch Mat: chiefly sunny southerly to westerly slopes and cliff ledges. Limited.
Herb Mat.	Grass Mat: snow-flushed sites, moist sandy situations, or in association with scrub; usually sheltered.
Scrub.	Willow Scrub: sheltered situations, generally on sandy or talus soils in glens with abundant but not late snow cover. Limited (Pl. XVIII, phot. 5).

From the more detailed summary here given it will be seen that the local types, as previously indicated, have collectively a climatic and individually a microclimatic significance, but are also determined in their occurrence by the factors grouped under the head of geomorphology. Some of the more restricted types, notably Rhacomitrium-Moss Mat in the untypical form in which it is found at low levels here, Vaccinium Mat, and to some extent Alectoria Mat, are largely so conditioned, and may be regarded as quasi-climax rather than climax types from the climatic standpoint.

It should also be borne in mind that under the influence of this combination of factors, and particularly in a transition region such as Isersiutilik, variants are necessarily common which do not fall directly under any one of the types individually. Every possible combination is found under the combined influence of microclimate and geomorphology, and two examples are given below from field notes. The first is a portion of a preliminary transect in which the effect of microrelief is pronounced:

Yards	Approximate type	Details of variant
50	Empetrum-Birch Mat	*Empetrum* dominant with some *Betula* and heath willows
8	Sedge Bog	*Eriophorum angustifolium* with *Salix chloroclados* associated
20	Ledum-Birch Mat	Erect, closed *Betula* and some *Ledum Groenlandicum*. Lichen-covered rocks protecting
12	Rock fjaeld	Crustaceous lichens
2	Empetrum-Moss Mat	*Empetrum* markedly dominant
25	Mixed Ledum-Birch and Birch-Lichen Mat	Cladinae, *Stereocaulon* and other lichens numerous with *Betula*, *Ledum* and scattered heath willows
75	Mixed Empetrum-Moss and Empetrum-Birch Mat	*Empetrum* abundant in mixed community with *Betula*, some *Ledum* and many lichens, as *Cladonia* spp.

The second example, from an altitude transect along a shoulder running up north-north-west to the main block of Ivisat, will show more clearly the interplay of factors, and will at the same time form the transition to the montane vegetation which is the subject of the next section.

Altitude ft.	Conditions	Vegetation
200	Hollows between rock domes, aspect S.E.	Ledum-Birch Mat with much *Cladonia alpestris*: *Empetrum*, *Vaccinium*, Heath Willows scattered, but flourishing
300	Ridge of weathered rock domes	Alectoria Mat, *Empetrum* persisting below on north-east slope; *Saxifraga oppositifolia* here
250	Streamlet in depression	Vaccinium Mat, about 60 cm. Heath Mat of reduced Scrub Willows
300	Shelving southerly slope	Mixed vegetation with *Vaccinium uliginosum* f. and *Juniper* on rock ledges, flourishing
350	Ridge of weathered rock domes	Flanked by Alectoria Mat: first bare patches on crown
	Depression in corridor floor. (Site of dried out pond in the past)	Grass Mat of *Calamagrostis* and *Deschampsia* among Turf Hummocks, flanked by luxuriant *Empetrum*
	Exposed corridor crown	Practically bare
400	East side of shoulder, now exposed to north-east winds by gap south-east of Ivisat. (Wind now E.N.E.)	Alectoria Mat, but *Vaccinium* f. or var. and *Betula* still form low mat in hollows
450	Aspect east-north-east	Increase in lichens, *Empetrum* persisting in numbers, but stunted
500	Corridor floor, running down south east	Dwarf Herb Mat, with *Salix herbacea* present, passing in more sheltered parts into normal Grass Mat: *Phleum alpinum* present. Vaccinium Mat on north side of corridor
600	Level ground; col leading to main block	Birch-Lichen Mat with some *Calamagrostis* persisting, passing into Alectoria Mat with greater exposure
620	Exposed flats, bare locally	Diapensia Mat Barren, with *Solorina crocea* in bare places
650	Weathered ridge, aspect south east	Alectoria Mat with *Vaccinium uliginosum* var. *microphyllum* and *Rhododendron Lapponicum*, *Stereocaulon* persisting

This transect was carried up to Ivisat summit: the results, together with those of the other altitude transects are summarised below.

(4) *Orographic types* (Pl. XX, phot. 8).

Mountains. Open herbaceous vegetation of the Polar type seems general from the lists of summit and nunatak species given by Porsild and cited by Warming (**53**); cf. also Grenfell, Labrador (**58**), and Summerhayes and Elton, Spitsbergen (**65**), who cite cryptogams.

High Fjaeld shows great local variation in Godthaab Fjord. To eliminate this as far as possible data were taken from ascents of south-westerly slopes, representing the optimum development of vegetation, though levels and plateaux had to be included.

(a) *Cloudy type.*

Upper Montane Zone. Open vegetation, diminutive and extremely sparse or absent on the windy summit flats, especially so in snow hollows. *Luzula confusa, Poa glauca, Saxifraga rivularis, S. comosa, Cardamine bellidifolia* and *Oxyria reniformis* characteristic phanerogams, or locally *Phippsia algida* and *Cerastium trigynum* on bare earth. *Polytrichum alpinum* and *Bryum Oxoniense* (see Dixon (**29**)) the dominant mosses, locally the sole vegetation, with *Pohlia gracilis*, abnormal *Rhacomitrium fasciculare*, Hepaticae (*Marsupella apiculata*

and *Anthelia Julacea*) and the common lichen *Solorina crocea*. Other mosses, such as *Rhacomitrium hypnoides* and *Conostomum tetragonum* occur, but other lichens, except for *Cetraria* and *Stereocaulon* spp. and *Cladonia pyxidata*, are negligible. The following local types were distinguished:

No vegetation.	Snow gullies and some northerly exposures.
Open.	Poppy-Herb Barren: traces on ridges.
	Solorina-Moss Barren: dominant on plateaux.
	Luzula-Moss Barren: frequent on earth pockets.
	Oxyria-Herb Barren: areas on slopes locally.
Moss Mat, more or less open.	Salix-Moss Mat: traces.
Lichen Mat, more or less open.	Alectoria Mat: poor and traces.

Noticeable are the peculiar bryophyte population, the absence of *Dryas integrifolia* and *Cassiope tetragona* and the great scarcity of lichens, even the rocks being often naked but for *Andreaea crassinervia*, while on the soil beneath even algae as *Zygnema* and diatoms can be found. The specific composition is one of maritime, late snow and Schneetälchen types, and the extremely barren appearance probably due to wind-packed snow, protecting in winter but lasting late.

Middle Montane Zone. Open Mat where soil allows, but extremely variable. *Salix herbacea* the commonest dwarf shrub, or locally *Dryas integrifolia* with broad leaves approaching f. *intermedia*; *Vaccinium uliginosum* var. *microphyllum* entering, but other shrubs sparse and scattered (*Empetrum, Cassiope* spp., and *Diapensia* chiefly). *Sibbaldia procumbens, Lycopodium alpinum* and *Polygonum viviparum* the commonest herbs, with *Poa alpigena, P. glauca, Luzula* and *Carex* spp., and locally bright flowers as *Arnica alpina, Veronica saxatilis* and *Cerastium alpinum*. *Rhacomitrium hypnoides* the chief of the mosses which include *Polytrichum strictum* var. *alpestre* f. *arctica, Drepanocladus uncinatus* f. and var. *orthothecioides* acc., and *Conostomum tetragonum*. The chief lichens are *Cladonia gracilis* var. *elongata, Cetraria hiascens* and *Lecanora squamaria*, but species numerous, including *Cladonia pyxidata, C. fimbriata, C. rangiformis* (?), *Stereocaulon paschale* and *Parmelia pubescens* (?), with *Solorina* persisting on bare patches. Local types:

Open.	Luzula-Moss Barren: mixed variants frequent.
	Oxyria-Herb Barren: ledges and gullies mixed.
Open Mat.	Dryas Mat Barren: easterly exposures, locally extensive.
	Diapensia Mat Barren: traces in mixed vegetation.
Moss Mat.	Salix-Moss Mat: extensive in valleys or dominant.
	Rhacomitrium-Moss Mat: extensive on detrital slopes.
	Empetrum-Moss Mat: traces in earth pockets.
Lichen Mat.	Cladonia Mat Barren: extensive, especially high up.
	Alectoria Mat: poor on some exposed knolls.
Herb Mat.	Dwarf Herb Mat: often extensive in valleys.

As is natural in passing out of the inferred cloud zone, variants are here much mixed, with very many species, especially in the corries, comprising elements both of the upper and lower zones and a few intrusions (e.g. *Cassiope*

tetragona) from the more sunny continental highlands. Only the more conspicuous local types are given. Exposure is still sufficient for hardy species as *Chamaenerium latifolium* to be reduced to 7 cm. in height, and the most southern types, as *C. angustifolium*, are still absent. Late snow indicators (as *Salix herbacea, Lycopodium alpinum, Cassiope hypnoides* and even *Bryanthus coeruleus*, cf. (**68**)) are frequent and numerous in species still, and grasses and other herbs are generally plentiful, as in the maritime regime of the coast, whose appearance is here closely approached.

Lower Montane Zone. Moss Mat, passing into Open, Lichen, Patchwork or even Heath Mat according to aspect and exposure, as shown under local types below, with corresponding variations in the chief plants. *Salix herbacea* persists especially on north slopes, but *Dryas integrifolia, Rhododendron Lapponicum, Diapensia lapponica* and *Vaccinium uliginosum* var. *microphyllum* characteristic, the last becoming general. *Empetrum* and Knoll Willows are present, with other lowland shrubs, *Empetrum* being the commonest of these on westerly aspects, but giving place to *Vaccinium* and stunted *Betula nana* to the east and south, while *L. decumbens* is the less scarce of the *Ledum* spp. *Sibbaldia* and associated herbs persist, with *Trisetum spicatum* and other grasses (as *Deschampsia flexuosa* and *Agrostis borealis*). Xerophytes such as *Juncus trifidus, Luzula spicata* and *Potentilla tridentata* are frequent, and *Carex rigida*, or var., is general. The mosses are *Rhacomitrium hypnoides* and *Dicranum* and *Polytrichum* of the lowland type. Of the lichens, now numerous and varied, *Cladonia gracilis* or var. persists and some humicolous crustaceous types (*Lecanora tartarea* var *frigida* and *Candelariella vitellina* var. *aurella*), but *Cetraria hiascens, C. aculeata, Alectoria nigricans, A. ochroleuca, Sphaerophorus melanocarpus* and various *Cladonia* spp. are more common, with *Cladonia sylvatica, C. mitis* and *Stereocaulon paschale* of the elements of Cladina Mat. The chief local types are:

Open.	Oxyria-Herb Barren: few steep northerly scars.
Open Mat.	Cladonia Mat Barren: local patches, now closed.
	Dryas Mat Barren: some easterly talus exposures.
	Diapensia Mat Barren: chiefly hill tops and wind gaps.
Moss Mat.	Salix-Moss Mat: mixed except in late snow hollows.
	Rhacomitrium-Moss Mat: chiefly westerly exposures.
	Empetrum-Moss Mat: chiefly northerly and westerly lees.
Lichen Mat.	Cetraria Mat: mixed on some northerly exposures.
	Alectoria Mat: hill tops and easterly exposures.
	Birch-Lichen Mat: traces on southerly slopes.
Heath Mat.	Vaccinium Mat: westerly corridors and flush slopes.
Herb Mat.	Dwarf Herb-Grass Mat: some sheltered pockets.

Traces of the patchwork Empetrum-Birch Mat and even of Willow Scrub reduced to Heath Mat level begins to appear at lower levels between 100 and 400 m., ascending higher up the southwest slope of each succeeding hill inland. At the same time late snow plants, such as *Salix herbacea*, and even *Bryanthus*, begin to be thrust round to north slopes, where are found the last pockets in

Phot. 9. Terrace Vegetation: Low Willow Scrub on formerly eroded slopes of Kugssuk Head silt terrace. An "active" silt polygon with partly buried *Equisetum arvense* on it in foreground. In the background dry and almost uncolonised gullies of the present erosion cycle.

Phot. T. G. L.

Phot. 8. Montane Vegetation: the diminishing open mat of the Upper Montane Zone of Sunny High Fjaeld; arctic hare in centre of boulder-strewn terrain. *Cassiope*-Mat-Barren type; very stunted *Betula* and *Empetrum* still persist with plateau willows. Photo. Itulialik at 550 m.

Phot. T. G. L.

TRAPNELL—GODTHAAB FJORD

which Salix-Moss Mat retains its typical ground layer of *Dicranium molle*. Bare ground is restricted to the most exposed talus and the latest snow sites (*Pellia neesiana* and diatoms appeared to occupy such a site). *Vaccinium* and *Empetrum* are still generally stunted, *Betula* 5 cm. to 20 cm. at most, and *Ledum decumbens* 3 to 16 cm. This condition should be contrasted with the corresponding zone of the sheltered Ilulialik slopes described in the following section.

(b) Sunny type.

Upper Montane Zone. 800–600 m.: open vegetation on slopes with *Cassiope tetragona* the chief dwarf shrub, and lichens, especially crustaceous types, common (E. M. N.). Plateaux more barren, though *Oxyria* and associated Schneetälchen herbs (as *Saxifraga rivularis*, *Ranunculus pygmaeus* and the maritime (**37**) *Phippsia algida* and *Cerastium trigynum*) found here on the earth of probable snow pockets.

600–500 m.: much Open Mat, with *Cassiope tetragona* the physiognomic dominant over much ground; scattered *Dryas integrifolia* (some approaching f. *intermedia*) and *Rhododendron Lapponicum*: sparser *Diapensia lapponica*, *Vaccinium uliginosum* var. *microphyllum* (with even the lowland form entering in pockets), and Plateau Willows. *Salix herbacea*, *Cassiope hypnoides* and herbs of the preceding sub-zone restricted to presumed late snow hollows. Typically the herbs are xerophytic, especially on talus knolls (e.g. *Carex nardina*, *Juncus trifidus*, *Potentilla nivea*, *Draba hebecarpa* var. *norvegica*): *Hierochloe alpina* is frequent and even *Calamogrostis* accompanies the lowland *Vaccinium* in depressions. The common mosses are *Rhacomitrium hypnoides* and *Polytrichum alpinum*, but these are less conspicuous than the numerous lichen species, especially *Alectoria ochroleuca*, *Sphaerophorus melanocarpus*, *Cladonia mitis* and *C. rangiformis* of the white Cladinae, with some *Cetraria hiascens* or spp. in depressions. The variants of the lower sub-zone were much mixed, representing the following local types:

Open.	Oxyria-Herb Barren: pockets on plateaux.
	Luzula-Moss Barren: mixed patches of this type.
Open Mat.	Dryas-Diapensia Mat Barren: frequent patches.
	Cassiope Mat Barren: dominant on S.W. slopes (Pl. XX, phot. 8).
Moss Mat.	Salix Moss Mat: some plateau pockets and corridors.
	Rhacomitrium-Moss Mat: local and mixed on plateaux.
Lichen Mat.	Alectoria Mat: large patches on S.W. slopes.

Here as in the subcontinental region, *Dryas, Rhododendron, Diapensia* and the *Vaccinium* var. attain their greatest frequency in descending order, but in this case, there being no cloud zone and less snow, they ascend higher than *Empetrum*. However, the most plentiful and characteristic dwarf shrub is the *Cassiope*, whose seed was already mostly shed by the first week of July. It showed frequent signs of desiccation, and Mr T. M. Harris informs me of its dependence on winter snow cover under a corresponding regime in East

Greenland. Other plants, such as *Vaccinium*, are stunted, and the lichens numerous but small. Notable absentees were *Sibbaldia*, *Poa alpigena* and *Lycopodium alpinum* of the plants of the Cloudy High Fjaeld, and other late snow plants were practically absent from the southerly slopes. The general facies is of a dry and stony country, compared by T. G. L. to a Thibetan desert.

Middle Montane Zone. Predominantly Lichen Mat vegetation, but much mixed, as the transition zone between highland and lowland types. *Salix herbacea* persists with *Vaccinium* f. or var. in the corridors, but the *Cassiope* has been thrust round to more northerly slopes, and *Empetrum*, *Betula* and some *Ledum* (the last too stunted for field determination) are becoming general with the *Vaccinium* var. on the slopes. Typical herbs are the *Hierochloe*, *Trisetum spicatum* and *Potentilla tridentata*, but a favourable ledge will hold surprising lowland species (e.g. *Coptis trifoliata*, *Veronica alpina*, etc.). Mosses are small and concealed by lichens except for cushions in flushed patches which hold the *Tofieldia palustris* typical in such situations. The lichens are those named above, with more *Cetraria nivalis*, Cladinae and other *Cladonia* spp., too numerous for full enumeration in the short time available for this part of the reconnaissance. Variants observed were of the following types:

Moss Mat.	Salix-Moss Mat: damp corridors only.
	Empetrum-Moss Mat: restricted or mixed.
Lichen Mat.	Alectoria Mat: extensive in upper part.
	Birch-Lichen Mat: lower part, mostly stunted.
Patchwork Mat.	Empetrum-Birch Mat: restricted and untypical.
Heath Mat.	Vaccinium Mat: stunted, only in turfy corridors.

Herb Mat and scrub associates are present only as scattered individuals, the uppermost limit of the typical lowland complex being here placed at 250 m., and, as previously stated, lower nearer the ice cap. Comparison should here be made with the Lower Montane Zone of the subcontinental region. It may also be noted that in this descent we have had a fairly clear "zonation," so far as the term is applicable in Greenland, typified by the series Cassiope Mat Barren—Alectoria Mat—Birch-Lichen Mat with less extensive types such as Empetrum-Moss Mat, giving a climatic series comparable to that by which transition is made from the continental High Arctic to the continental Low Arctic. In the present zone, subject to differences in snow cover, water supply becomes a master factor, the sun having full effects on the southerly escarpment. Herbs such as *Trisetum* are purple with anthocyanin. The late snow types disappear, *Oxyria* finding its last stronghold (with *Arabis alpina*) at the moistest cliff foot, where the snow must lie longest, and *Salix herbacea* similarly disappears in the moistest gullies. In the low "heath" *Betula*, *Vaccinium* and *Ledum* spp. are still stunted, but the full Low Arctic complement of species is entering.

Lower Montane Zone. There is little difference here from the normal continental Low Arctic. The greatest luxuriance was found on the south-westerly

slope, where descent is made from the beginnings of Empetrum-Birch Mat found in the last zone, through shelves of Ledum-Birch Mat to Willow Scrub pockets standing in tall *Calamogrostis* and other grasses, such as *Poa alpigena*. Especially down the sheltered gorges, the grass shelves are refreshingly green, with rare southern plants such as *Pirola secunda* and *Habenaria albida* among the numerous associated herbs. The tops of the willows and alders are often out of reach overhead. But on easterly escarpments, and especially on the upper shoulders of the dry silt terraces, the complex changes back to the steppe type, and transition is made from Birch-Lichen Mat, to deep Cladina Mat, with stunted shrubs and a few xerophytic herbs such as *Hierochloe*. The flats beneath are intermediate in character between the two aspects described in this paragraph.

(5) *Lowland physiographic types* (Pl. XX, phot. 9, Pl. XXI, phots. 10, 11).

Low fjaeld. The observations cited hitherto refer to rocky substrata, so that little comment is called for under this head, except as regards the plants of the prisere. The heavily denuded gneiss here usually provides a comparatively water-retaining surface, with little mineral soil, favouring numerous partially lithophytic mosses such as *Rhacomitrium hypnoides* and *Dicranum elongatum*. On the drier exposures various chasmophytes, as *Saxifraga aizoon* and spp., *Campanula Gieseckiana* and *Woodsia ilvensis*, are common, while the rock surface is covered by numerous crustaceous lichens (*Lecanora, Rhizocarpon, Acarospora* and *Lecidea* spp.) and *Gyrophora hyperborea*. Between the rock exposures a thick raw humus soil is developed, 18–26 cm. deep in the heath, and this is favoured by the dwarf shrubs, notably by *Empetrum*, but also by *Vaccinium uliginosum* f. and *Betula nana*.

The probable normal succession is from lithophytic lichens to mosses, notably the turf-building *Rhacomitrium Lypnoides* and *Dicranum* spp.: these become densely encrusted with lichens, especially *Cetraria*, and later *Cladonia* spp., *C. sylvatica* and *C. alpestris* being among the first of the Cladinae to appear. The whole moss slab, with its embedded hepaticae, is thus killed, and provides the turf in which the lichen or dwarf shrub cover develops, *Pohlia* and *Polytrichum* spp. persisting in the cracks of the lichen slabs, and *Drepanocladus uncinatus* under the dwarf shrubs. In the case of willow scrub the succession is of a more hygrophytic character. Where exposures of softer rock have been left, fissured to talus by the frosts, the soil is drier and stonier, the lichens increase, and chomophytes such as *Potentilla tridentata* and *Juncus trifidus* are common. The normal succession is in this case from few lichens, chiefly *Alectoria* spp., and chomophytic herbs such as *Silene acaulis*, to mixed lichen mat in which *Alectoria, Sphaerophorum* and *Cetraria* spp. overrun the few small mosses (*Pohlia* and *Polytrichum*), *Cladonia mitis* and *Stereocaulon paschale* being among the first elements of Cladina Mat to appear. Of the dwarf shrubs, *Vaccinium uliginosum* var. *microphyllum* enters early, and in

more favourable places, *Betula nana*. But the hard gneiss is the normal substratum, and as it restricts the downward growth of the roots of the dwarf shrubs (which are frequently 1·25–1·75 m. in length), a spaced growth and the formation of patchwork heath are encouraged.

Silt terraces. From the lithosere with cryptogamic pioneers we pass through the intermediate chomosere to the silt seres with a herbaceous prisere. In the terrace areas the chomoseral type is represented only on sandy river gravels, the wash-out of the terraces, where *Stereocaulon denudatum*, *Rhacomitrium canescens* and some other mosses, and herbs such as *Chamaenerium latifolium* and *Artemisia borealis* are among the pioneers, and *Carex rigida* var. *concolor* becomes common. But on the normal terrace the pioneers are herbs, the eroded slopes having much *Potentilla tridentata* with *Juncus trifidus* on the sandier parts and *Rumex acetosella*, *Poa glauca*, *Trisetum spicatum* and *Chamaenerium* spp. About or on the polygons of the more clayey terraces *Equisetum arvense* is the pioneer, and is a recognised clay-tolerant species. Other *Equisetum* and *Juncus* spp., especially *J. castaneus*, and sedges, especially *Carex capillaris*, and *Pedicularis euphrasioides* are characteristic of the species which follow. *Equisetum sylvaticum* and *Carex capillaris* persist in heath subject to polygon disturbance, and in such ground the cryptogams are poor or discouraged, with the exception of *Aulacomnium turgidum*, *Pohlia cucullata* and *Peltigera rufescens*.

It appeared that the disturbances of the ground or the amount of clay in the baked surface soil prevented succession from advancing very far beyond the herbaceous prisere, there being little accumulation of humus. In the climax, in the absence of maintained polygon processes, as on the sandier terraces, the lichens are generally dominant, the deep percolation drainage, and exposure of the flat surface to winds, leading to drought and shallow snow, and favouring lichens by comparison with the dwarf shrubs. In the Cladina Mat, *Stereocaulon paschale* and *Cladonia mitis* are the chief species. *Betula nana* tends to be restricted to the snow-catching aligned depressions attributed to solifluction curves, except where the terrace is sheltered. Here again the humus layer is shallow and ill-decomposed, and it is probable that its average depth on these terraces is only 5–7·5 cm. The colluvial mineral soil beneath discourages *Empetrum*, but *Vaccinium uliginosum* var. *microphyllum* and *Ledum decumbens* remain fairly frequent, and grasses such as *Hierochloe* are encouraged. Moreover, where snow cover and water supply are adequate, the various willows and the alder are greatly encouraged, and if conditions do not allow of scrub, there is generally a quantity of heath willows in company with the other dwarf shrubs, the *glauca* types predominating in the hybrid population. The one example of pure alder scrub seen had arisen at the foot of an eroded terrace. Taking the terraces seen as a whole, it may be said that Birch-Lichen Mat of a poor or mixed type is characteristic, but that Cladina Mat, often unmixed, is the more extensive on the sandier and

Phot. 10. Drainage Basin: area of turf hummocks overlying detritus blocks and riverine gravels. *Vaccinium* Mat dominant, *Salix chloroclados* in the runnels and some hybrids with *S. glauca* on the hummocks. Flowers of *Chamaenerium latifolium* indicate gravelly substratum.

Phot. 11. Sinking Shoreline: *Elymus arenarius* var. *villosus* growing on edge of subtidal zone, on former heath turf partly overturned by ice-thrust. Inside to the left *Festuca rubra* is dominant in the neutral zone.

TRAPNELL—GODTHAAB FIORD

more stable terraces, and here attains its maximum development, as was also noted by Rosenvinge in the south (**51**).

Drainage basins. The pioneers in the hydrosere are numerous diatoms, *Navicula viridis* vars., *Tabellaria flocculosa* and *Eunotia arcus* being the most general, together with other lesser algae of which the genera *Cosmarium* and *Staurastrum* are dominant. Significant of the small influence of the climatic factor on this group is the fact that, except for fewer and smaller individuals, the diatoms of the Upper Montane Zone of the continental region differed from those of the lowlands in only one point, the greater relative frequency of *Navicula borealis*, exactly as noted by West for Scottish mountains (**71**). In either case *Zygnema* spp. are the larger algae on stones, with *Drepanocladus uncinatus* associated alike in Upper Montane snow pools and in Maritime and Low Arctic lowlands. In the lowlands the variety *fluitans* of this moss was common, with *Calliergon sarmentosum* or its rarer variety *pseudostramineus*, while *Hippuris vulgaris* was the commonest of the aquatic plants in either region in permanent ponds, with *Sparganium hyperboreum* in drying ponds. But in the bogs, while *Drepanocladus scorpioides* and spp. are generally the dominant mosses, the *Eriophorum* spp. vary.

In the Upper and Middle Montane Zones of the subcontinental region, and, curiously enough, on manured ground in the Maritime Arctic coastlands and in the silt terrace bogs, the Arctic *E. Scheuchzeri* is regular, whereas both Maritime Arctic and the other Low Arctic bogs in Godthaab Fjord have the more southern *E. angustifolium*. It would appear from this that *E. angustifolium*, as also *Empetrum* and some other dwarf shrubs of the heath, cannot stand a mineral or nitrogen-rich soil, and that the arctic species is thus enabled to replace it in such situations. The other sedge associates in the lowlands are *Carex rariflora* and *Scirpus caespitosus*, but all these are commonly reduced to 5–15 cm. in height on the coast, as against anything up to 75 cm. in the interior. Close to the coast *Carex rariflora* may form a kind of moor in association with *Salix chloroclados*, which flourishes here, or the two may grow on turf hummocks with the willow on the south side of each hummock. Inland and away from the shore *Carex rigida* var. *concolor* is a common associate of *S. chloroclados* in such situations, especially on a substratum of alluvial sand.

As a later stage in the succession, *Vaccinium uliginosum* f. and *Drepanocladus uncinatus* or spp. form a common covering of the turf hummocks. Finally the higher and drier hummocks are crowned each by about two plants of *Betula nana*, often with a bush of *Ledum Groenlandicum* arising in the middle, while the *Vaccinium* is relegated to the sides and the *Salix* to the interstices of the hummocks. But this further development, and also scrub-crowned hummocks, are only found in the more favoured interior of the fjord. It must be remembered, too, that the majority of the hummock systems have not arisen by any rapid successional process, for the cores of the hummocks

are composed of a peat which pollen analyses show to date right back to the warm "post-Glacial" period, and that the reconstruction of any primary sere, in a country with a climate and history as chequered as that of Greenland, is at best a hazardous undertaking.

Shoreline. The submerged algae of the salt water were not studied, but reference must be made to the extensive beds of *Zostera marina* found in about a metre's depth of water on silt shoals arising from the erosion of the Kugssuk terraces. The plants were much encrusted by the bryozoan *Hippothoa hyalina*, and appeared to have no algal associates. Indeed the outfalls of the terrace streams appeared to be devoid of algal life, being clouded with suspended silt (cf. (**51**)), though the upper parts of the shoreline here showed consocies of *Juncus arcticus* and *Triglochin maritimum*.

On the normal shoreline the three zones noted are more pronounced. *Puccinellia phryganoides* is the common species in the tidal zone on sand or mud. The subtidal zone on these substrata has an association of *Carex glareosa*, often dominant, *Triglochin maritimum* and *Potentilla egedii*, *Elymus arenarius* var. *villosus* entering also on sand or on turf overturned by ice-thrust (Pl. XXI, phot. 11), while *Plantago borealis* and *Stellaria humifusa* are found among the rocks. In the neutral zone are found on mud *Bryum acutiusculum*? (see Dixon (**29**)) and *Carex rariflora* with some of the halophytes, on sand generally *Festuca rubra*, in rock crevices *Sedum roseum* and *Saxifraga decipiens*, and in the marginal heath turf *Calamagrostis Langsdorffii* and scattered patches of *Cornus suecica* and *Lomatogonium rotatum*. These observations apply particularly to the Kugssuk inlet. Further up the fjord the water becomes sweeter and the plants here cited for the tidal and subtidal zones tend to disappear, till at Majuala the *Elymus* was the only plant of halophytic tendencies noted. Throughout, where the rocks are steep, there is a naked band at high water mark kept free of algae by ice-scour or a late-lasting ice-foot.

IV. SUMMARY.

1. The vegetation of Godthaab Fjord is described in relation to that of other parts of West Greenland, and with special reference to an area intensively surveyed about Isersiutilik.

2. The fjord is divided between two main climatic "regimes," with Isersiutilik occupying an intermediate or subcontinental position:

Maritime Arctic. Coastal region with cool, humid, foggy or cloudy summer: much snow, but exposed to sea winds: delayed thaw.

Low Arctic. Continental region with warm summer and strong insolation, but with greater temperature extremes: shallow snow driven by strong easterlies: rapid and early thaw accelerated by "foehm" winds.

Isersiutilik. Subcontinental Low Arctic, with warm, semi-humid summer, sunny, with local cloud regions; moderate snow and variable winds, at least in summer: thaw probably rapid.

The highlands are grouped into a cloudy type in the maritime or sub-continental regions and a sunny continental type.

3. The influence of climate is paramount, the dominant factors being held to be (*a*) insolation and snow duration and (*b*) snow depth, the variations in water supply associated with the latter factor also being important in the continental region. But owing to the great local variation in these factors produced by microrelief, and to other geomorphic influences, there is no one climatic climax in any one region. In its place there is a complex of variable local types.

4. If hydroseral and haloseral vegetation be excluded, the direct influence of physiographic factors is slight, the underlying rocks all belonging to one geologic system. There is, however, a tendency for the vegetation to become progressively more continental in character as transition is made from the local types of denuded gneiss to those of talus, sand and silt. This effect is most marked on the silt terraces, which carry the most pronounced type of continental lichen vegetation, but the more clayey examples have also a number of plants such as *Equisetum arvense* and *Carex capillaris* particularly addicted to them.

5. From a comparison of climatic and orographic types of vegetation it seems that the regional types, here and in other parts of Greenland, fall under the following heads:

Open vegetation predominantly herbaceous with *Papaver nudicaule, Luzula confusa, Oxyria reniformis, Saxifraga* spp., etc., or with *Rhacomitrium hypnoides* and other smaller mosses such as *Polytrichum alpinum, Bryum* and *Pohlia* spp., and few lichens such as *Alectoria* and *Cetraria* spp. or *Solorina crocea*. This open vegetation is Polar or Maritime High Arctic or High Montane in distribution.

Open Mat vegetation with various dwarf shrubs, such as *Dryas integrifolia*, or more extensively, *Cassiope tetragona*; less extensive, *Rhododendron Lapponicum*, with very various scattered herbs including xerophytic grasses, such as *Poa glauca*, and *Luzula* or *Carex* spp. with some small mosses as *Dicranum elongatum* vars., *Polytrichum* and *Pohlia* spp. and *Conostomum tetragonum*. These are generally obscured by lichens, especially *Cetraria* and *Alectoria* spp., with various *Cladonia* spp. present. The mosses and lichens are fewer and *Rhacomitrium hypnoides* is more plentiful under cloudier regimes nearer the coast. The Open Mat type has on the whole a High Arctic and Continental Montane distribution.

Moss Mat. The dominant mosses are *Rhacomitrium hypnoides* or *Dicranum* spp., as *D. molle* and *D. elongatum* and other species found in Open Mat. Lichens are rare, with the exception of *Cetraria hiascens*. The chief dwarf shrubs are *Empetrum hermaphroditum* or *Salix herbacea*, with *Vaccinium uliginosum* f. or var. often associated. Herbs are plentiful, including *Carex* spp., and especially grasses, as *Deschampsia flexuosa, Festuca ovina* var. or

Agrostis borealis and *Trisetum spicatum*, with various late snow species such as *Sibbaldia procumbens*. Distribution, Maritime Arctic, or Low Montane in cloudy regions.

Lichen Mat. The lichens are especially *Cladonia mitis*, *C. alpestris* and *Stereocaulon paschale*. Mosses are scarce except *Pohlia nutans* and *Polytrichum juniperinum*, *Betula nana* and *Vaccinium uliginosum* var. *microphyllum* are the chief dwarf shrubs; *Empetrum* is scarce and *L. decumbens* is the chief species of *Ledum*. Herbs are scarce except a few xerophytic *Carex* or *Luzula* spp., and the characteristic grass *Hierochloe alpina*. Continental Low Arctic in distribution, or Low Montane in sunny regions, and encouraged by dry silt terraces.

Heath Mat vegetation of *Ledum Groenlandicum*, *Betula* spp., or *Vaccinium uliginosum* f., with scattered *Salix glauca* hybrids and scattered herbs including grasses such as *Calamagrostis Langsdorffii*, *Poa alpigena*, etc., and occasional southern species as *Hieracium lividorubens*. Moss undergrowth of hypnoid types, such as *Drepanocladus uncinatus* and *Hypnum Schreberi*. Lichens are typically scarce with the exception of a few *Cladonia* and *Peltigera* spp. This vegetation is not widely represented, and only occurs in more favoured places. It appears to be subcontinental Low Arctic in distribution, and links on with the scrub and forest ecotone of Eurasia and America.

The species cited in the above characterisations are only examples of those which seem important from the present survey, and typical of the physiognomy. The vegetation forms given are not regarded as finally defined but are intended to show how the classification, treated from the standpoint of climatic regimes in the body of this paper, may ultimately be put on a simple physiognomic basis.

6. The local types are a replica in miniature of these major types, for both the latitude gradient of precipitation or snow depth, and temperature total, and the fjord gradient of insolation, snow duration and temperature maximum, are reproduced in the differences resulting from changes in aspect and exposure according to microrelief. This may be seen by a comparison of the following regional and local types in Godthaab Fjord:

Regional vegetation forms	Local types
Open vegetation	Poppy-Herb Barren
	Solorina-Moss Barren
	Oxyria-Herb Barren
	Luzula-Moss Barren
Open Mat	Dryas Mat Barren
	Diapensia Mat Barren
	Cassiope Mat Barren
Moss Mat	Salix-Moss Mat
	Rhacomitrium-Moss Mat
	Empetrum-Moss Mat
Lichen Mat	Alectoria Mat
	Birch-Lichen Mat
	Cladina Mat
Heath Mat	Vaccinium Mat
	Ledum-Birch Mat

These may be treated as typical local vegetation forms of the regional types referred to above. The detail of local effects will be given in a subsequent paper on Isersiutilik, but the distribution of the dominant local types in the fjord and altitude gradients are summarised in the diagram below:

MONTANE. Cold and exposed

```
                          Poppy
                          Herb
                          Barren
                            |
        Solorina————————Luzula————Dryas/Diapensia
         Moss              Mat            Mat
        Barren            Barren         Barren
              /          /    \         /
        Salix——Rhacomitrium    Cassiope——  ——Alectoria
         Moss      Moss         Mat            Mat
         Mat       Mat         Barren
            \      /                  \      /
        Empetrum——  ——Empetrum————Birch
          Moss          Birch        Lichen
          Mat           Mat          Mat
           /             |             \
       Vaccinium        Ledum         Cladina
         Mat            Birch          Mat
       (drainage        Mat          (silt
        basins)          |          terraces)
                       Willow
                       Scrub
```

MARITIME. Late snow and cloudy

CONTINENTAL. Early snow and sunny

LOWLAND. Warm and sheltered

Distribution of local types in Godthaab Fjord.

Special types, such as the flush conditioned Oxyria-Herb Barren, Dwarf-Herb Mat and Grass Mat (which may be varied in their origin apart from dependence on snow water), and less understood types such as Cladonia Mat Barren and Cetraria Mat, are omitted here; but their microclimatic and soil requirements will be dealt with in a later paper. The lines indicate the principal transitions found between the local types in the altitude and fjord gradients.

No attempt is made to show an exact altitudinal zonation, for it was found that the point at which a given transition might take place fluctuated by as much as 300 m. according to aspect and exposure. It will be seen that the altitudinal gradient of vegetation types bears comparison with the latitudinal gradient.

The terminology of local types is not treated as a final one: for example it is possible that Alectoria Mat might elsewhere be found to have Sphaerophorum or Vaccinium more important, or that it would be better to speak of Empetrum-Cetraria Mat and Vaccinium-Birch Mat. Such points require investigation by subsequent expeditions in other parts of the Arctic. Subject to possible corrections of this sort it will be seen that regional and local types

in combination provide a means of mapping climatic regimes in regions where the maintenance of meteorological stations is difficult and their sampling error large.

7. It is shown that the area round the expedition's base at Isersiutilik represents an ecotone between Moss Mat and Lichen Mat with tendencies towards heath mat. It has therefore a very large number of local types represented producing very complex vegetation, but making the locality an exceptionally good one for an intensive survey of a biocoenose representative of the western land belt as a whole.

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NOTES ON THE VEGETATION OF THE VENEZUELAN LLANOS

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CONTENTS.

En una palabra, esos llanos, que Humboldt nos pintó como uniformes en su aspecto, ofrecen infinitas variaciones en su misma monotonia. PITTIER, 1920, p. 18.

I. INTRODUCTION.

IN the course of recent entomological field-work on behalf of the Imperial Institute of Entomology and the Empire Marketing Board my wife and I had the good fortune to follow the route of Humboldt and Bonpland not only in the northern part of Venezuela but also south across the *llanos*, those extensive plains so much described but so little known botanically and ecologically. Perusal of the available literature, cited at the end of this paper, and discussions with Dr H. Pittier of Caracas, whose *Manual de las Plantas Usuales de Venezuela* is invaluable to the visiting naturalist, showed that the composition of the llano vegetation is almost entirely unknown. Pittier writes (1920, p. 16) that the descriptions of the llanos by Humboldt, Codazzi and Sachs are concerned chiefly with the physical aspect, so that "we remain in almost complete darkness as to the details of their flora" (translation). In 1929 (p. 456) he states that "we know scarcely a dozen species from the Lower Llanos, including the few recognised along the Orinoco by previous travellers" (translation). This must be my excuse, as an entomologist, for venturing into the field of pure plant ecology. It should, however, be mentioned that I was intensely interested in the grass associations as supplying alternate and primitive hosts for the sugar-cane borer (*Diatraea saccharalis*) and other cane pests. For the rest I made such observations as my botanical knowledge and the time available allowed.

I am deeply indebted to Dr H. Pittier for much kind help and advice, including the determination of some of the plants and the submission of others, especially grasses, to the U.S. National Herbarium. For other determinations I am alone responsible. Dr A. Jahn generously allowed us to use his magnificent library of works on Venezuela.

It should be strongly emphasised that the aspect of the llanos here described is that of the dry season—the long dry period which, in opposition to the general rule, the Venezuelans call "summer" (*verano*). I was in the llanos at the end of December (1930) and the beginning of January (1931)—thus well in, but not at the height of, the dry season (November to April).

II. Itinerary.

The route, which may be picked up easily on any map of Venezuela, led from Caracas in a westerly direction almost to the eastern end of the Lake of Valencia, and then southward through Villa de Cura, San Juan de los Morros, Ortiz, and Calabozo to our destination, San Fernando de Apure. There is now a magnificent road to Valencia, and a good one to Calabozo; but thence southward a car can go only in the dry season, and then with considerable difficulty, "shimmying" for many miles over sun-cracked dried mud, with no well-defined way. Humboldt and Bonpland, 130 years before, and Sachs, some fifty years ago, took essentially the same route. Pittier (1929) followed it as far as Calabozo. Schimper seems only to have touched the edge of the llanos, but I know practically nothing of his itinerary.

III. Historical.

The earliest account that I have seen of the llano vegetation is that of Lope de La Puebla, who journeyed up the Orinoco and the Apure in 1521 and founded San Fernando de Apure, still one of the chief towns of the llanos. Albéniz de la Cerrada (p. 228) describes the explorers' impressions on landing opposite the future site of San Fernando de Apure and pushing northward over the great plains:

"Crossing the bare silt at the water's edge, they entered the zone of high grass. The horsemen were almost hidden in the sea of vegetation, which presented the greatest obstacles to their advance. It took all the strength of the horses to push a way through the thick growth of interlacing stems, tangled inconceivably, as though this was the first time that the agitations of man had creased a furrow in that millennial calm, under the impassible serenity of those skies" (translation).

As we shall see later, this is a graphic description of the zone of *Paspalum fasciculatum*, which La Puebla, from internal evidence in Albéniz's account, saw considerably later in the dry season than ourselves.

The chronicler goes on to state that had Nature clothed all these extensive plains with such vegetation the horsemen might just as well have turned back

to their ships. They came, however, into country where the grass was of a different kind "that is to say, shorter and less dense." This was a region of lagoons and ponds. Later they found extensive palm groves, and everywhere they noticed the absence of stones.

But the manuscript of Maestre Diego Albéniz de la Cerrada was only recently published, and the first to introduce the llanos to European readers was Humboldt, whose classical description is well known, and still remains the chief source for physical data. He writes, "all around us the plains seemed to ascend to the sky, and the vast and profound solitude appeared like an ocean covered with sea-weed....Through the dry mist and strata of vapour the trunks of palm-trees were seen from afar, stripped of all their foliage and their verdant summits, and looking like the masts of a ship descried upon the horizon....There is something awful, as well as sad and gloomy, in the uniform aspect of these steppes. Everything seems motionless; scarcely does a small cloud, passing across the zenith, and denoting the approach of the rainy season, cast its shadow on the earth. I know not whether the first aspect of the Llanos excite less astonishment than that of the chain of the Andes" (**2**, 84, 85).

There is little that Humboldt records of the vegetation. He notes (p. 105) that the llanos he traversed were principally covered with the following grasses[1], *Killingia monocephala, K. odorata, Cenchrus pilosus, Vilfa tenacissima, Andropogon plumosum, Panicum micranthum, Poa repens, Paspalum leptostachyum, P. conjugatum, Aristida recurvata.* This must be regarded rather as a collector's list than a catalogue of dominant species[2]. "Mingled with these gramina some plants of the dicotyledonous class are found; as turneras, malvaceae, and, what is very remarkable, little mimosas with irritable leaves...." He mentions the occasional occurrence of solitary llanera palms and groves of this tree mingled with a species of *Rhopala (op. cit.* p. 106). He describes also the groups of moriche palms (*Mauritia flexuosa*) which flourish in the wetter areas.

Mendoza, in 1846, published a sociological study of the llanos, in which the physical and biological data were taken almost entirely from Humboldt.

Ramón Páez, son of the celebrated general, who was educated at Waterton's old school in England, made the acquaintance of that naturalist and was inspired largely by Waterton's *Wanderings* to write, on his return to his native plains, a book on the llanos (see References) which was first pub-

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[1] *Killingia* (*Kyllinga*) is, of course, a sedge.

[2] Thus, for instance, he says "at this [dry] season, near Calabozo and San Jerome del Pirital, these grasses scarcely attain the height of nine or ten inches. Near the banks of the Apure and the Portuguesa they rise to four feet in height, so that the jaguar can conceal himself among them, to spring upon the mules and horses that cross the plain." In these two cases it is entirely different grasses which are concerned, the dense high beds of the Apure and Portuguesa consisting, at least at this season, almost exclusively of *Paspalum fasciculatum*, which apparently does not occur near Calabozo.

lished in 1862, in English. There is much that is purely anecdotal in the work, but it does present an intimate picture of the pastoral life of the llanos.

C. Sachs, the physiologist, made a stay of some months at Calabozo to study the electric eel, on the spot where Humboldt made his classic observations. Sachs (1879) published a book which contains little detailed information on either the fauna or the flora of the llanos. There is a good figure of a *Copernicia* palm enveloped by a strangling fig (*Ficus*) as described below.

Schimper (1898) describes the llanos as "usually a typical savannah, in some places with very scattered trees, in others with more densely crowded trees. According to my own observations, high forest occurs as fringing forest along the water-courses; savannah forest occurs at the foot of the Cordilleras on the coast, *pari passu* with an increasing rainfall, and also in moist depressions in the ground, in the same way as in the campos." I cannot agree that the forest fringing the llano-side of the coastal Cordillera is well called "savannah forest," nor is there any evidence that the rainfall there is greater than in the llanos themselves, but rather the reverse, as indicated by a frequent transition into quite arid thorn forest.

Warming (1909, pp. 297, 298) describes the llanos as a special type of savannah, where trees are few or even wanting, "save in the moistest places, where palms, including *Mauritia flexuosa* and a species of Corypha, together with other plants, give rise to forest, which does not itself really belong to savannah...." This is slightly misleading in that the Corypha (*Copernicia tectorum*) does not grow in the moist places, and must be regarded as almost an essential element of the typical llanos.

Pittier gives to the geographer, Codazzi (whom I have not had an opportunity to consult), the credit of noting that the term "llanos" includes savannahs of many diverse types. Pittier himself (1920, 1926, 1929) has stressed our ignorance of the elements of llano vegetation. In his own expedition to the llanos (1929) he paid most attention to the flora of the fringing forest.

Bews (1929, p. 294) refers to the scarcity of ecological information concerning South American grasslands. He is inclined to refer the Venezuelan llanos to the bunch-grass type of savannah. As we shall see later, the llanos include, however, not only both tall and low bunch-grass savannah but also true high-grass tropical savannah, at least near the Rivers Apure and Portuguesa.

IV. Physical features and climate.

The physical features and climate of the llanos have been described at considerable length by Humboldt and by Sachs.

These vast plains are entirely of Quaternary and alluvial formation (Shanahan, 1927), the soils varying from gravels to silts, approximately as one passes from north to south. The total absence of stones in the lower llanos,

"en una extensión de más de doscientas leguas castellanas," was a cause of great wonder to the first Spanish explorers in 1521.

The elevation of the llanos is in general no more than 250–300 ft. above sea-level (Humboldt, **2**, 88). The altitude of Calabozo is 100 m., and that of San Fernando de Apure, 73 m.

The most marked climatic feature is the very long drought-stricken season (November to March) rendered still more detrimental to vegetation by the dry north-east wind. The rainfall is not high, that of Calabozo being 48 in. and that of San Fernando de Apure, 50 in. (Sifontes, 1928), but it is concentrated in the wet season, which is rendered still wetter by the wide inundations from the great rivers, the Orinoco and its tributaries, which, abruptly every year, change the means of transport over vast areas from horseback to boats. At this time, according to Humboldt (**2**, 139) "the horses that wander in the savannah, and have not time to reach the rising grounds of the Llanos, perish by hundreds. The mares are seen, followed by their colts, swimming during a part of the day to feed upon the grass, the tops of which alone wave above the waters." Unfortunately few naturalists appear to have visited the llanos in the wet season.

Schimper (1903, p. 277) describes the llano climate as one *hostile to woodland*. He says there is a quite rainless season of five months, during the greater part of which the dry easterly trade wind blows almost continuously and usually with extreme intensity, and is associated with great heat and dryness of air. Such a dry season, he remarks, is unfavourable to woodland but does no harm to dried-up prairie whose existence is maintained only by the roots. And according to Humboldt it rains continuously during the rainy season, thus favouring grassland, which depends on very frequent showers.

V. APPROACH TO THE LLANOS.

In the southern foothills of the Coastal Cordillera there has been much clearing and modification of the vegetation by man and stock, particularly in the valleys. Some of the hilly open country is, however, original and typical *Andropogon-Curatella* savannah, varying from open grassland to *Curatella americana* L. in "orchard" formation. South of San Juan de los Morros one passes through large continuous areas of a low open type of forest. Some of this is definite thorn forest, with *Acacia macracantha* H. and B. dominant, but the larger area, consisting of taller, now largely leafless trees, approaches more to a monsoon type. The rainfall, of which there are unfortunately no records, can only be about 40 in., thus falling much below that required for monsoon forest in Schimper's definition (70 in.). It agrees better with his savannah forest, to which, indeed, he actually refers it (1903, p. 352), but I consider the term very misleading, since none of the typical savannah trees or shrubs, such as *Curatella, Bowdichia* and *Byrsonima* are present. It is

probably best to follow Troup (in Tansley and Chipp, p. 292) and call this merely "deciduous forest" until a better classification can be drawn up.

A few miles south of Ortiz the country begins appreciably to flatten out towards the south. One specimen of the llano palm, *Copernicia tectorum* Mart. appears in the still continuous low deciduous forest. These palms rapidly become numerous. Another mile or so and the real plains begin, but the view is shut in by the now much lower deciduous bush, which occasionally gives way to open grassland scattered either with thorn bushes (*Acacia macracantha* H. and B.) or with llano palms. At El Sombrero, where one crosses the River Guárico, one still has a wide view, from the high river bank, of almost continuous low deciduous forest in every direction. Along the river itself, probably owing to clearing and grazing, this is replaced by *Acacia macracantha*.

VI. The higher llanos (El Sombrero to Calabozo).

South of El Sombrero the road continues through the same type of deciduous forest, now all leafless, but brightened by the magnificent yellow flowers of an abundant tree, *Cochlospermum vitifolium* Willd. This is flat country which, after some miles, gives place to an undulating landscape clothed in savannah vegetation, dominated by the grass, *Cymbopogon rufus* Rendle, with scattered small trees of *Curatella americana* L. and *Bowdichia virgilioides* H.B.K. On the plains once more, which we hardly leave again, these low trees are spaced less widely to form parkland, which, however, is replaced after some distance by the low continuous deciduous forest marked by *Cochlospermum*.

After a further stretch of *Cymbopogon-Curatella-Bowdichia* savannah, wide grass plains appear, much grazed, almost imperceptibly undulating, some recently burned. They bear in places scattered llano palms (always *Copernicia tectorum*), in others brownish thorn bushes (not identifiable) and in still others *Curatella*. They might be called very open parkland or savannah. At times this passes into "orchard" country, with *Bowdichia* almost as common as the *Curatella*.

At Calabozo the River Guárico is crossed again. Its bare banks are fringed chiefly with thorn forest (*Acacia macracantha* dominating). A considerable pond had its flat banks grazed so closely that it was impossible to identify a single species in the herbage.

VII. The lower llanos (Calabozo to San Fernando).

The fringing thorn forest fades quickly into sparse *Cymbopogon-Curatella* savannah, the bushes and small trees of the latter widely scattered. Among the *Cymbopogon* is much of a blue-flowered Labiate, *Hyptis suaveolens* Poit. (*mastranto*). We are soon in a dried-up, dusty, extensive plain covered with *Cymbopogon* and *Hyptis* as overwhelming dominants, and no bushes. This

plain opens out still more and we see for the first time a view such as inspired Humboldt's classical description of the llanos—an apparently limitless expanse of low grass, as flat as the sea, with the hazy presence of a few scattered trees on one horizon only, barely discernible. This is evidently typical low bunch grass savannah. In places and over considerable areas the whitish sea of bleached *Cymbopogon* gives place to a larger reddish grass, *Andropogon condensatus* H.B.K., still mixed with *Hyptis*. Among both grasses the yellow flowers of *Hibiscus sulphureus* H.B.K. are fairly common. Now and again appears a small society of short white cottony grass (*Andropogon selloanus* (Hack.) Hack.).

Further on the sheer plains of *Cymbopogon* and *Hyptis*, extending to all horizons, are broken by small patches of bush, not larger than a quarter acre, some with the houses of those who tend the large herds of cattle and troops of horses. In some of these oases there are actually patches of bananas and of sugar-cane, the former exceedingly battered by the dry trade wind and the latter suffering badly from drought.

In places now the *Hyptis*, probably as a result of selective grazing on the part of the horses and cattle, which were introduced into the llanos in 1521 (Albéniz, p. 265) and 1530 (Mendoza, p. 31) respectively, grows in almost pure stands for miles.

Just past Los Bancos, llano palms appear again and with them low open deciduous forest, with a most unusual abundance of strangling figs (*Ficus* sp.). This, according to Pittier (1929, p. 459) is a new species. There seems to be a tendency for strangling epiphytes to appear in numbers in areas where other trees are either at the limit of their ecological range (ecotone) or are unable to grow at all. Thus a *Clusia* sp. and a *Ficus* grow luxuriantly, the former up to 20 ft. high, on the surface of the famous Pitch Lake in Trinidad.

The deciduous forest, in the midst of the llanos, showed the small tree, *Jacaranda obtusifolia* H.B.K. in magnificent flower. The bush *Helicteres guazumaefolia* H.B.K. was also blooming.

Lianes are very plentiful, and on the forest floor a frequent but not very gregarious *Bromelia* sp. A few column cacti (*Cereus* sp.) are the first seen for a long time.

For some miles after this the road lies through almost treeless plains again, with large areas, evidently almost swamp in the wet season, covered with short grasses of species distinct from those of the drier areas, and the bush, *Ipomoea crassicaulis*. There are occasionally actual lagoons, in one case fringed with *Thalia geniculata*, "wild" rice (*Oryza sativa* L.), some *Sacciolepis vilfoides* (Trin.) Chase, and beyond these a wide zone of the short grass, *Steirachne diandra* Ekm.

Curatella savannah intervenes again and passes into treeless plains of *Cymbopogon-Hyptis*. Near houses this becomes a dusty *Hyptis-Sida* association, with much of a tiny *Cassia* (*C.* (*Chaemaecrista*) *serpens*).

At Corozo Pando are extensive flats of *Ipomoea crassicaulis* growing very luxuriantly, and widely surrounding lagoons fringed with *Cyperus articulatus* L. and *Eleocharis geniculata* Vahl. eaten down wherever stock can reach. Further out are a few odd bushes and llano palms.

The lagoons are part of a *caño* which in the wet season forms a channel by which one can reach the Apure River in a launch.

South of Corozo Pando this caño wends its way between fringing forest. The typical fringing forest (*Galeriewald*) of the llano rivers is regarded by Pittier as true monsoon forest, the deficiency of rainfall being compensated by favourable edaphic conditions. This caño fringing forest consists, however, of small leafy trees, among which I recognise *Andira inermis* H.B.K. There are occasional palms, *Acrocomia sclerocarpa* Mart. (*Corozo*). The forest floor is entirely bare, save for a few dead leaves, I suppose owing to the inundations.

Outside the fringing forest the plain is now covered with low herbage, among which the grass, *Sporobolus indicus* (L.) R.Br., and the Labiate, *Hyptis suaveolens* Poit., are easily dominant. Later, though the *Sporobolus* remains the commonest grass, non-Gramineous herbs predominate, and we enter a sea of *Hyptis* extending almost to the horizon.

Some miles, and the llano palm (*Copernicia tectorum*) appears again, very heavily attacked by strangling figs, which, however, are absent when we enter the extensive palmetum of which these scattered palms are the heralds.

On its further side the palmetum passes rather abruptly into the Estero[1] de Camaguan, a wide open plain, clothed at first with much-grazed short grass and stunted rice (*Oryza sativa*) but later, right to the eastern horizon, with a pure knee-high stand of a much stouter grass with long trailing stems rooting at the nodes, and close, leafy sterile culms, erect and somewhat hirsute. Although no flowers were to be found, this grass is undoubtedly *Paspalum fasciculatum* Willd., with which I am familiar in Trinidad, and which has been recorded by Spruce as forming pure stands on river banks and practically never flowering (Chase, 1929, p. 177).

Sachs (p. 250) mentions a grass called locally "lambedora" as dominant in the Estero de Camaguan, which is a noted grazing area. *Paspalum fasciculatum* is, however, known as "gamalote"—a common name for stout coarse grasses in Latin America, and applied to Guinea grass (*Panicum maximum* Jacq.) in northern Venezuela. Gamalote is said to be entirely unpalatable, while *lambedora* is a favourite forage grass, noted for its tenderness (Páez, pp. 98, 109). They are therefore certainly not the same grass. But Páez (p. 98) states that the *gamalote* is regularly burned as soon as it is sufficiently dry, and it is apparently then that other species are able to cover the ground.

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[1] An *estero*, according to **Páez** (1929, p. 110) is a savannah which retains in its soil sufficient water to grow fresh forage throughout the year. The Estero de Camaguan seemed to me to be formed by the basin of a very wide and very shallow lagoon.

At Camaguan we reach the River Portuguesa, like the Guárico a tributary of the Apure. Apart from the fringing forest along this river, and one palmetum (*Copernicia*) near San Fernando de Apure, the route from Camaguan to the latter town, on the banks of the Apure, passes through practically nothing but vast plains of *Paspalum fasciculatum*, up to waist and even breast-high. Occasional damper areas and lagoons support stands of *Ipomoea crassicaulis*. On dryish areas there are stretches of *Malachra alceifolia* Jacq. The *Paspalum* covers dried, cracking mud. Rarely, among its close-growing sterile culms, appears a flowering stem of another, more slender grass, *Eriochloa punctata* (L.) Desv. Hamilt.

At the time of our visit the Apure River was low, with extensive sandbanks on which grew pure stands of a glaucous composite shrub, *Tessaria mucronata* D.C. Where the actual sloping silt banks of the river began, either at the water's edge, or separated from it by sand beaches, there began also extensive, pure, close stands of vivid fresh green *Paspalum fasciculatum*, evidently springing up on the cracking mud as the water receded. These *Paspalum* beds passed up the bank slope and on to the plains above, right to the horizon, either uninterruptedly or with occasional islands of bush of a fringing forest (*not* savannah) type. As it leaves the water's edge and passes into the older stands, this grass loses its fresh green colour and at the same time becomes somewhat more hairy, though never so hairy as *P. fasciculatum* normally is in Trinidad[1].

In places, especially on the flatter beaches, the front line of *P. fasciculatum* contained a few plants of other grasses, including *Panicum elephantipes* Nees, *Echinochloa polystachya* (H.B.K.) Hitch. and the little mat-grass, *Eragrostis maypurensis* (H.B.K.) Steud.

VIII. COMPARISON WITH THE SAVANNAHS OF GUIANA AND TRINIDAD.

There are in Guiana savannahs of two main types—the water-savannahs of the coastal belt and the upland savannahs of the far interior, 200–300 miles from the sea. I have not yet visited the latter, and am dependent almost entirely on the descriptions of Schomburgk (trans. 1922–3). Hitchcock (1922, p. 441) regards them as "an extension eastward of the vast savannahs of Venezuela." Their elevation Schomburgk gives as 350–400 ft. (**1**, 308). The surface is frequently undulating—whereas the llanos are strikingly level. Schomburgk mentions also areas "dotted here and there with bleak masses of granite from 10 to 600 ft. in height, a characteristic peculiarity that essen-

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[1] I have, however, found examples of *P. fasciculatum* in Trinidad (Tamana) quite as glabrous as the smoothest Apure specimens. Mrs **Chase**, moreover, in her monograph (1929, p. 177) mentions "nodes from glabrous to densely bearded" and in fact seems to recognise almost a complete variation from pilose to glabrous in other parts of the plant. Mrs Chase quotes a herbarium note by Spruce to the effect that the exceeding scarcity of flowering culms is due to constant nipping by goats; but this is quite inadequate to explain the infrequency of flowering throughout Trinidad and the llanos. The fact is, *P. fasciculatum* spreads so rapidly by creeping stolons that reproduction by seed has apparently become unnecessary.

tially distinguishes these grassy plains from those immense llanos and pampas of the southern portion of South America" (*loc. cit.*). There are, however, extensive level plains as well.

The rainfall, which may be in places as low as 46·2 in. (Harrison, 1925, p. 5) corresponds closely with that of the llanos, and differs greatly from that of the wet coastal savannahs, where the rainfall is rarely below 90 and may rise above 150 in. The upland savannahs and llanos are thus true climatic grasslands, while the wet savannah, and, as we shall see later, all the types of Trinidad savannah, are clearly not.

Schomburgk's account shows that scattered trees of *Curatella americana* and *Bowdichia* are rarely lacking, with isolated bushes of *Byrsonima* spp. and others. There are considerable oases of forest, however, attaining six miles and more in diameter, dominated in the wetter areas by *Mauritia* palms and Musaceae (including *Ravenala guianensis*) and in the drier spots fringed, among other bushes, by *Helicteres guazumaefolia*. Hitchcock records the following grasses as common or frequent on the upland savannahs: *Leptocoryphium lanatum, Paspalum abrahami, Arundinella hispida, Andropogon leucostachyus, Andropogon selloanus, Cymbopogon bracteatus, Heteropogon contortus, Trachypogon plumosus, Elyonurus adustus*. But Schomburgk, with an Irishism which the botany of his day would overlook, states that "the real grass-covering consisted for the most part of Cyperaceae; in fact the genera *Isolepis, Carex, Hemicarpha, Dichromena*, and several species of *Cyperus* had their home on the dry higher-lying savannahs, while *Mariscus, Kyllingia*, and *Scleria* occupied the damp and marshy spots. *Hypolytrum* was also represented" (**1**, 296). Such a predominance of sedges is certainly not characteristic of the llanos, and was nowhere seen in our traject.

On the route to Roraima Schomburgk mentions "6 to 7 foot high cutting grass and reed that covered a boundless plain" (**2**, 131). This is reminiscent of the coastal wet savannah, the "cutting grass" being probably a *Rhynchospora*. Nowhere else does Schomburgk mention tall grass, save (**1**, 278) when he first entered the Rupununi savannahs, and found, on the river bank, his view blocked by grass more than 6 ft. high. The bulk of the upland savannah is evidently of the short bunch grass type. Savannah fires were frequent, even in Schomburgk's time, being lit by the Indians to drive out game. He graphically describes the remarkably quick recovery after a sweeping fire. In a fortnight palms, bushes and "grass" are greener than before.

Martyn (1931) describes a savannah which is in some respects intermediate between the wet and the upland types. This is the Waranama savannah situated 80–90 ft. above sea-level, some 60 miles inland on the Berbice River. The open savannah is covered with grasses and sedges, among which predominate *Trachypogon plumosus, Axonopus aureus, Andropogon leucostachyus* and *Rhynchospora pterocarpa*. "The level of vegetation is broken at intervals by stunted bushes, chief of these being *Byrsonima coccolobaefolia* and *Curatella*

americana, which in certain areas become a dominant feature." "In swampy depressions, too wet for forest, the Aeta palm, *Mauritia flexuosa,* occurs; sometimes as a few scattered trees, elsewhere forming large belts of 'palm forest' similar to those found in the swamp savannahs near the coast." Sharply-defined islands of bush occur on the large mounds thrown up by leaf-cutting ants (*Atta* sp.). The vegetation on these hillocks shows definite succession, culminating in bush dominated by *Byrsonima spicata.* Finally there are patches of scrub known as "muris" on areas of white quartz sand. The chief small trees are *Clusia nemorosa* and *Byrsonima spicata,* and the commonest bushes, *Pagamea capitata* and *Houmiri floribunda* var. *guianensis.* Although this savannah considerably resembles the upland type, it is apparently of edaphic origin, and has more in common with certain Trinidad savannahs to be described later.

The wet savannahs of the coastal region in the Guianas and the Orinoco Delta are in some cases actually below sea-level. They form exceedingly sharply demarcated areas in the swamp forest which covers most of this region. In extent they vary from the slightly open margins of forest creeks to wide stretches ten miles or more across, sometimes interspersed with islands of forest occupying rising ground. In some cases it is possible, during the dry season, to walk across them dryshod, where during the wet season there may be several feet of water. Schomburgk (**1**, 173) calls them "swampy grass-flats." There is often a "vegetable decking" to use his term, which is strong enough to bear the weight of a man, but sways under his feet, over an abysmal morass. Such a type passes of course, into true swamp, and is called "savannah" in accordance with tropical usage, only to denote the absence of trees. The larger water savannahs, like that at Moruka, are dotted with oases of rain forest, occupying spots of higher ground, which form the sites of Indian settlements. Elsewhere, as in the Orinoco Delta, where we explored the Carapo and Awaracaba savannahs, there is an uninterrupted sea of sedges, fringed by aeta palms (*Mauritia flexuosa* L.f.) and then passing into the dominant swamp forest which covers most of the 12,000 square miles of the Delta.

I should think that on a moderate estimate 95 per cent. of the vegetation in the larger Guiana and Orinoco wet savannahs visited consisted of the so-called "savannah grass," a coarse brownish sedge (*Rhynchospora* sp.) growing up to a height of 6 ft. Marking the passage of a creek there are sometimes however fairly wide stretches of the grass *Sacciolepis striata* (L.), and a fine-leaved sedge, growing in deeper water, with considerable white *Polygonus* sp., *Eleocharis geniculata,* a clambering *Mikania,* and small beds of luxuriant grasses, *Hymenachne auriculata* Willd. and *Panicum elephantipes* Nees. None of these last, however, are true savannah elements. Often, though, the true savannah sedges extend to the edge of the open water.

In the British Guiana savannahs the sedges, again near the waterways, are sometimes interspersed with coarse ferns, Crinums and odd, undersized,

sickly specimens of *Montrichardia arborescens* Schott. In the savannah fringe the bush, "fat pork," *Chrysobalanus pellocarpus* often forms pure stands.

How far the above description applies or formerly applied to the coastal savannahs further east, is doubtful, for those which I have seen are profoundly modified by draining and grazing. Further east still, in Nickerie, Dutch Guiana, are extensive swamps of *Typha angustifolia* L., with curious islands of *Erythrina glauca* Willd., the trees apparently rising not from higher ground but from the sea of bulrushes itself.

To sum up, the wet savannahs are not grasslands at all, but sedge-covered, and they differ further from the llanos and the upland savannahs in being of edaphic or topographic origin.

The Trinidad savannahs, under the lee of the Northern Range, are entirely edaphic in origin. The soils, according to Hardy, "consist of greyish white sand varying in depth from one to four feet—underlaid by a more or less clayey substratum of a mottled red, orange, grey and brown appearance." They "appear to be the much-leached residues of previously deposited material." The hummocky surface is waterlogged during the rainy season and unduly dry at other times. By their vegetation these savannahs may be divided into two main types, the one probably related to the upland savannahs of British Guiana and the other reminiscent of, though drier than, the wet savannahs of Guiana and the Orinoco Delta. The first kind, exemplified by the Piako (Piarco) and Mausica savannahs, shows a dominance, save in wetter spots, of grasses over sedges, the abundant species being *Trachypogon plumosus* H. and B., *Paspalum pilosum* and *Thrasya robusta*. The first of these grasses is said to be common on the upland savannahs of British Guiana. The woody vegetation is of the orchard type, and consists very largely of *Byrsonima crassifolia* H.B.K. and *Curatella americana*. In other places cocorite palm (*Maximiliana caribaea*) is easily dominant, the erect bush, *Coccoloba pubescens*, and an *Andropogon* are common, and large beds of the Musaceous herb, *Heliconia psittacorum*, appear. In wetter spots more sedges enter, and a few iris-like tufts of *Paspalum densum* Poir. Small savannahs of similar appearance may be seen in the Northern Range itself between 700 and 1500 ft. above sea-level. Here the dominant grass is usually either *Trachypogon plumosus* or *Thrasya robusta*—seldom a mixture; but a clambering sedge (a wide-leaved *Scleria*) and a coarse grass, *Axonopus equitans*, are often common, and the dominant shrubs, *Curatella* and *Byrsonima crassifolia* are intermixed to a varying degree with other species.

The second main type of Trinidad savannah is exemplified by the southern part of the Aripo Savannah, and is marked by a greater abundance and variety of sedges (including a *Rhynchospora* sp.) and by the presence of the highly characteristic aeta or moriche palm (*Mauritia setigera*). These palms, with the other woody vegetation, tend to be segregated into islands standing out of the sea of sedge and grass, among which occur a number of interesting terres-

trial orchids, bladderworts and sundews, and in places a straggling tangle of *Cassytha americana*. The smallest islets, of a few bushes only, consist almost invariably of *Clusia nemorosa* solely. In slightly larger patches *Symphonia globulifera* joins the company, and in drier parts, *Byrsonima crassifolia* and a *Bactris* palm. The large "islands," containing a variety of rain-forest trees, are overtopped by *Mauritia* palms, seedlings of which spring up thickly from the undergrowth of breast-high sedges (coarse, cutting species, including a stout *Scleria*) interspersed with a few melastomes. These larger "islands" are edged, as often in the Orinoco Delta, almost continuously by bushes of "fat pork" (*Chrysobalanus pellocarpus*). In the "islands" a rather rare pigeon (*Columba rufina* T. and K.) breeds commonly and it is recorded also by Schomburgk from similar oases in the upland savannahs of Guiana.

IX. EFFECTS OF MAN AND STOCK.

Concerning the effects of fire on climatic grasslands, whether lit by lightning or by man, a considerable amount has been written; but less seems to be known of its influence on edaphic savannahs. On a spur of the Trinidad Northern Range, facing me as I write this, is a small upland savannah of the kind described in the text, with very sharply marked edges. It shows up as a yellowish green patch in the deeper green second-growth rain-forest which surrounds it. Regularly every year this slope is swept by fierce fires. Their effect on the savannah is not noticeable—the vegetation a few weeks afterwards seems unchanged. The rain forest, on the other hand, is annually destroyed and is represented in the meantime by low bushes and herbage. These, however, are all members of the first stage in the succession to true rain forest. Were the fires prevented, they would apparently and in time completely regenerate the original forest. There is no evidence that the annual fires are enabling the savannah to encroach on the forest to the least degree.

Beebe describes the origin of a wet savannah on the Abary River as due to fire. He writes (1910, p. 358): "All this savanna was once a densely wooded jungle of mora trees, eta palms and other growth. In 1837 a drought occurred of such extent that all the vegetation—trees, palms, and underbrush—became dry as chips. The inevitable followed and a fire started in some way which swept this whole region, reaching in places even to the Demerara. Then floods came, broke through the loosened barrier and tangled roots, and infiltrated through the soil. Grass and reeds took the place of the great moras, and now, almost to the horizon, stretches the flat, open expanse of marsh."

There can be no question that fires have been much more frequent on the llanos and the other savannahs mentioned since the advent of man and especially of civilised man. Even in the recesses of the Orinoco Delta, there was evidence that the smallest savannahs on uninhabited creeks were burned by wandering Indians more or less annually. On the llanos Páez and others mention regular annual burning of the coarser grasses. It may be that the

great height and tangled growth of the Apure grasslands as noticed by La Puebla in 1521 were due to a lesser incidence of fires at that date, since it seems that the height reached nowadays is distinctly less. But yet the original vegetation was adapted to sweeping fires before the discovery of America.

A change of probably considerably greater influence was the introduction of close-grazing European animals—horses and cattle—which now roam the llanos in tremendous numbers and constitute the chief wealth of Venezuela. Compared with their widespread, close, and selective grazing the effects of the small llano deer and, on pond and river margins, of capybaras, must have been ecologically almost negligible. Both horses and cattle, as we have seen, were introduced well before the middle of the sixteenth century. During the dry season much of the plains is obviously overstocked. We found the wide margins of many ponds and streams eaten as smooth as a billiard table. Undoubtedly the vast areas, in the drier localities, of the aromatic Labiate *Hyptis suaveolens*, and, in wetter places, of the Convolvulaceous bush *Ipomoea crassicaulis*, are due to selective feeding on the part of the stock, and represent a by no means negligible deterioration of the llanos as pasture.

Nearer the rivers, however, within the zone of the high grass (*Paspalum fasciculatum*) and on the *esteros*—that is within the range of the deeper annual inundations—the influence of stock on the original composition of the vegetation is much less, partly since the period of grazing is also limited, and partly because the other ecological conditions are so severe and so specialised. Thus *Hyptis*, which does not enter this zone, presumably cannot survive the annual deep inundations, while *Ipomoea crassicaulis* is excluded, save from pond margins, by the aridity of the dry season.

X. Summary.

1. The llanos between the Coastal Cordillera and the Apure River consist for the most part of *bunch grass savannah*, as the term is used by Bews (1929), of a type intermediate between his *tall* and *low* classes but tending largely towards the latter. The dominant grasses are *Cymbopogon rufus* over very large areas, and over smaller but still extensive areas, *Andropogon condensatus* and *Sporobolus indicus* respectively. An induced dominance of the Labiate, *Hyptis suaveolens*, due to selective grazing, prevails over large tracts. The incidence of trees on the llanos themselves, apart from the fringing forest of the rivers, varies from nil to a fairly dense scattering of the orchard type, the predominant species being *Curatella americana* and *Bowdichia virgilioides*. Llanera palms (*Copernicia tectorum*) vary in frequency in the same way. Aeta palms (*Mauritia flexuosa*) occur in damper spots, but were not seen on our traject.

2. To a varying distance from the Rivers Apure and Portuguesa there extends a wide zone (some miles) of true *high grass savannah* marked, at least in the early dry season, by an overwhelming dominance of the coarse grass, *Paspalum fasciculatum*. This high grass savannah is dependent less on annual burning—which all the llano suffers—than on the deep annual inundations.

It is thus more specialised and not quite of the same origin as that characterised by Bews (1929, p. 292).

3. Throughout the llanos one encounters damper depressions and ponds with a zonal vegetation of their own, described in the text, and different from that of the surrounding plains.

4. The upland savannahs of British Guiana are bunch grass savannahs resembling the llanos in vegetation save for a greater preponderance of Cyperaceae, and of similar climatic origin, but often differing widely in topography.

5. The water savannahs of the coastal regions in Guiana and the Orinoco Delta are, in the first place, not grasslands at all, but predominantly sedge-covered. They are of topographic or edaphic origin, rather than climatic.

6. The drier savannahs of Trinidad agree closely with the upland savannahs of British Guiana, so far as the descriptions of the latter allow us to judge; but they are of purely edaphic origin.

7. The wetter savannahs of Trinidad recall those of the coastal mainland, and are apparently of similar origin.

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THE VEGETATION OF MORABALLI CREEK, BRITISH GUIANA: AN ECOLOGICAL STUDY OF A LIMITED AREA OF TROPICAL RAIN FOREST[1]. PART I

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(*With Plate XXII and six Figures in the Text.*)

CONTENTS.

I. INTRODUCTION.

THE aim of the ecological work undertaken by the Oxford University Expedition to British Guiana[2] was to be intensive rather than extensive. After only fifteen weeks of field work the most we could hope to do was to give an accurate, and as far as possible, quantitative description of the vegetation of our chosen area. It was clear that we could only raise problems and not solve them.

Though one of us had some years previous experience of the Guiana forest, which was valuable in suggesting lines of work, it must be emphasised that our results and conclusions apply only to the limited area we studied and not necessarily to the whole Guiana forest, still less to rain forests in general.

The greater part of the field work was carried out by both authors jointly, but the writing of this paper was done by the junior author only, who must

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[1] Part of the results of the Oxford University Expedition to British Guiana, 1929.

[2] For a general account of the work of the expedition, see (**1**).

take the responsibility for the views expressed in it, though the manuscript was read and, for the most part, approved by his collaborator.

All plants for which actual specific names are given in our tables were collected (unless otherwise stated) and a complete set of specimens will be found in the Kew Herbarium.

For the determination of species we have to thank Mr N. Y. Sandwith of Kew, who was a member of the Expedition and co-operated with us in the field. For help in naming certain groups Mr Sandwith wishes to acknowledge the help of Mr A. H. G. Alston of the British Museum (ferns and Lycopods), Dr Max Burret of Berlin-Dahlem (palms), Dr H. A. Gleason of New York (Melastomaceae), Dr Anton Heimerl of Vienna (Nyctaginaceae), Dr A. S. Hitchcock of Washington (grasses), Dr J. Lanjouw of Utrecht (Euphorbiaceae), Dr L. B. Smith of Harvard University (Bromeliaceae), Dr T. A. Sprague of Kew (Bignoniaceae), Mr V. S. Summerhayes of Kew (Orchids), Dr W. Trelease of Urbana, Illinois (Piperaceae) and Dr R. E. Woodson, Jr. of the Missouri Botanical Garden (Apocynaceae).

Accounts of new and critical species are given in a series of papers in the *Kew Bulletin* (**2, 3**).

We are indebted to the Director of Agriculture, British Guiana, for the data on which the account of the climate of our area is based. We have to thank Mr R. R. Follett-Smith, Chemist-Ecologist to the Department of Agriculture, British Guiana, for examining and reporting on our soil samples, Mr G. Udny Yule, F.R.S., for advice on certain statistical points and Mr E. E. Pochin for working out the statistical treatment of the data in Table VI.

To Prof. E. J. Salisbury, F.R.S., Dr H. Godwin and various members of the British Guiana Forestry Department, who were kind enough to read our manuscript and offer useful criticisms, our best thanks are also due.

We have to thank Major R. W. G. Hingston, M.C., for permission to reproduce some of his photographs.

Finally, we should like to thank our Arawak Indian helpers, especially Mr Jonah Boyan, whose wide and accurate knowledge of the forest flora was invaluable.

An account of the ecology of the bryophytes is being reserved for another paper.

II. The habitat.

(1) *The position and topography of area.*

The colony of British Guiana lies on the north-eastern coast of South America between the latitudes of 0° 50′ and 9° 0′ N. It includes three main regions:

(i) A strip of alluvium, mostly less than 30 km. wide: much of this land is below sea-level and defended by dykes. Where the ground water is salt or brackish, mangrove swamp (dominants, *Avicennia nitida* Jacq., *Rhizophora* spp. and *Acrostichum aureum* L.), where it is fresh, swamp forest of various

types (including the so-called "Swamp Savannah," dominated by *Mauritia flexuosa* L., the Ité Palm) are the natural vegetation. By far the greater part of the population is concentrated in this alluvial strip, all the towns and most of the villages lying within it, and much of the land is now cultivated. The chief crops are cane sugar and rice.

(ii) A large slightly elevated region of igneous rocks including the greater part of the total area of the colony and extending to the frontiers of Brazil, Venezuela and Surinam. The surface is always gently undulating or hilly, but rarely reaches a height of more than 300 m. The most of this area is covered by an unbroken rain forest, continuous with the vast forests of the Amazon basin to the south and of the Orinoco to the west. It is crossed by several large rivers of which the Essequibo, with its great tributaries the Mazaruni and Cuyuni is the chief. Falls or rapids caused by dykes are found on all these rivers at points never far from the sea and have largely prevented colonisation and exploitation of the interior. There is an extremely scanty population of aboriginal Indians and there are a very few civilised settlements.

(iii) In the far interior there are high plateaux and sandstone mountains, the highest of which is Roraima (2664 m.). Much of this region is grassy savannah, but the proportion of the interior not covered with forest[1] is now known to be far less than is suggested by the accounts of Richard Schomburgk (4) and other early travellers. Some of the savannahs are used for cattle ranching. Nearly all the third region and much of the second are inadequately explored and mapped.

The area which was studied intensively by the Oxford Expedition was that easily accessible by canoe and on foot from a base camp on the bank of Moraballi Creek about 3 km. above its junction with the Essequibo river. It was only 6° 11′ (about 650 km.) north of the Equator and about 50 km. within the coastal edge of the rain forest. The other localities whose vegetation was examined were all within 40 km. of the base camp and situated on the banks of the Essequibo, Cuyuni and Mazaruni rivers.

Moraballi Creek is a small fairly fast-flowing river rising on the Demerara-Essequibo watershed, having a more or less westerly course of about 24 km. It is fed by a great number of small streams. It is a typical "black-water"[2] creek, as are its longer tributaries, but the shorter ones (i.e. those rising not as far back as the main watersheds) are often "white-water" creeks (clear or muddy, but uncoloured).

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[1] **Barrington Brown (5, p. 6)** in 1875 estimated the total area of the whole colony under forest at about 90 per cent.

[2] The water of such creeks is chocolate brown by reflected and mahogany by transmitted light: it appears faintly coloured in a test-tube. It is perfectly clear, but shows the Tyndall effect with beams of sunlight. It has a peculiar taste. In Guiana all such creeks rise as springs in the Wallaba forests of the white sand ridges (see Part II) and the coloration is locally considered to be derived from the dead leaves of the Wallaba tree. "White water" creeks always rise in forest of other types.

The surface of the area is low, but nowhere flat except in the swampy alluvial land near the Essequibo and the narrow strips along the main creek and its biggest side creeks. The greater part of it is undulating and rises gently towards the watersheds. The Demerara-Essequibo watershed is a ridge about 100 m. high; the Moraballi-Wineperu watershed on the south and the Moraballi-Kamakabra on the north are lower. From these main watersheds many smaller spurs, mostly about 50 m. high, branch off and in places reach the bank of the main creek. These ridges are often very steep-sided though flat-topped, and the streams draining them usually run through deep gullies with nearly precipitous banks.

The underlying rock of the whole district, as of most of the colony, is granite or gneiss, perhaps with some greenstone, v. (5), but outcrops are uncommon except in the banks and beds of the creeks. In one place, however, steep rocks about 4 m. high were met with in the forest. The steeper hillsides are often strewn with boulders. In the gullies large masses of ferruginous sandstone are exposed, but they are concretions formed secondarily from the soil, not native rocks.

The soils met with in the area were remarkably varied. The higher ridges are always topped with a thick layer of coarse, pure white sand. The stream valleys have a silt, or sometimes a sandy, soil. Passing from the streams towards the ridges, heavy red clays, then red loams, finally brown sands, are met with successively before reaching the white sand. The characteristics of these soils will be described in detail in Part II. Common to all of them is deficiency in lime and high acidity (lowest acidity of samples pH 4·43). The red soils are probably siliceous laterites. All these soils are probably derived from the underlying granite (but see Part II).

(2) *Climate.*

There are no data about the climate of Moraballi Creek itself, but there has been for many years a well-equipped meteorological station at H.M. Penal Settlement, River Mazaruni, only 27 km. in a direct line from the base camp of the Oxford Expedition, and there are also some meteorological data for Bartica which is 3 km. nearer[1]. Though the climates of Moraballi Creek and of the Penal Settlement are undoubtedly very much alike, it is possible that some of the factors, in particular the rainfall, may differ quite considerably in the two places, since it is known that there are large local variations from place to place within the colony; for instance, the average annual rainfall for the years 1920–3 at the Penal Settlement was 255·7 cm., while on the other bank of the Mazaruni at Bartica only 4 km. away it was 178·6 cm.[2] The data

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[1] It must be remembered that both these stations are situated in large clearings and therefore record the *general* climate to which the forest is exposed, not its *internal* climate.

[2] There were more rainy days in the months September to November in 1929 at Moraballi Creek than at the Penal Settlement. This suggests that in regard to rainfall at least the climate is like that of the Penal Settlement rather than that of Bartica.
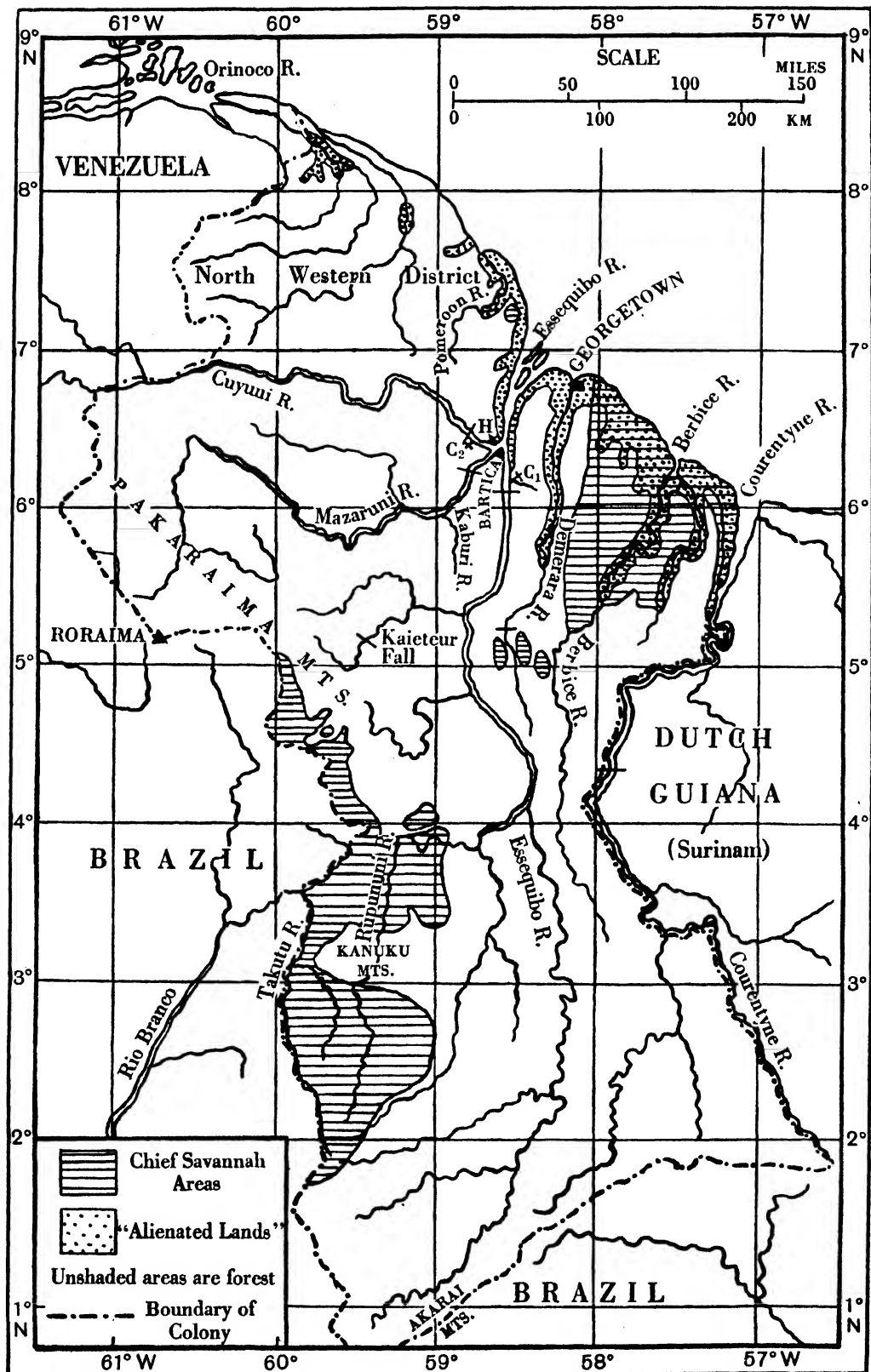
for the Penal Settlement will, however, give a sufficiently good general picture of the climate of our area. Apart from slight local variations the climate of all the rain forest in the colony is very similar as far as the available data show. The coastal region has a somewhat different, and the savannah regions a very different, climate. The Guiana rain forest in general has a climate like that of most other equatorial rain forest regions though there are small peculiarities.

Climatic factors:

(a) *Temperature.*

The temperature is high and very equable. It is higher during the dry seasons than during the wet, the hottest month being October and the coolest January, but the range of mean temperatures for the different months of the year is actually very small, much smaller than the range between night and day, though even that is always less than 10° C. Fig. 2 shows the variation of the monthly mean, and average monthly maximum and minimum temperatures during the year. The mean maxima, it may be noted, are not much higher than the maxima occasionally reached even in England and are much lower than maxima commonly reached in the sub-tropics. The absolute maximum for the years 1920–9 was 33·3° C., the absolute minimum 16·4° and the mean 25·9°. With these figures may be compared those for Manáos[1] (lat. 3° 8′ S.) in the Amazonian rain forest—mean 27°, average extremes 37° and 21°, daily range about 8°—and for Duala in the Cameroons (lat. 4° 3′ N.) which are typical for much of the rain forest of the Old World tropics—mean 25·5°, average extremes 32·8° and 20°, daily range averaging about 6°.

(b) *Rainfall.*

The mean annual rainfall for the years 1920–9 was 267·0 cm., but in the tropics especially the distribution of the rainfall is more important than the total amount from the ecological point of view. There are two wet seasons, one long (May to August) and one short (December and January). The autumn dry season, though the longer, is the less dry. No month has a mean rainfall of less than 10·7 cm. In the dry season during our stay at Moraballi Creek, we noticed that showers were very much more common about midday than at any other time. One moderate shower kept the forest undergrowth dripping wet for the remainder of the day and all the following night. It is therefore likely that in the drier months the numbers of days with rain are important

[1] All the data for places outside the colony are taken from **Brooks** (6).

FIG. 1. Sketch-map of British Guiana. The base camp at Moraballi Creek is indicated by C_1, the camp at Akaio Landing by C_2: H marks the position of H.M. Penal Settlement. The cross-lines on the rivers indicate a few of the more important waterfalls and rapids. "Alienated Lands" (i.e. alienated from the crown) include all the cultivated area, though they are not necessarily cultivated. We are indebted to Mr L. S. Hohenkerk for some of the data on which this map is based.

in determining the character of the vegetation. The number of days in each month with a measurable amount of rain (average for 1920–9) is as follows:

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
17	12	13	10	20	24	22	18	15	16	15	23

The fact that the driest month of the year (April) has as many as 10 days with rain suggests that the vegetation is unlikely ever to suffer a serious shortage of water in an average year. There is, however, a great variation from year to year in the rainfall of any one month. The long wet season has never been
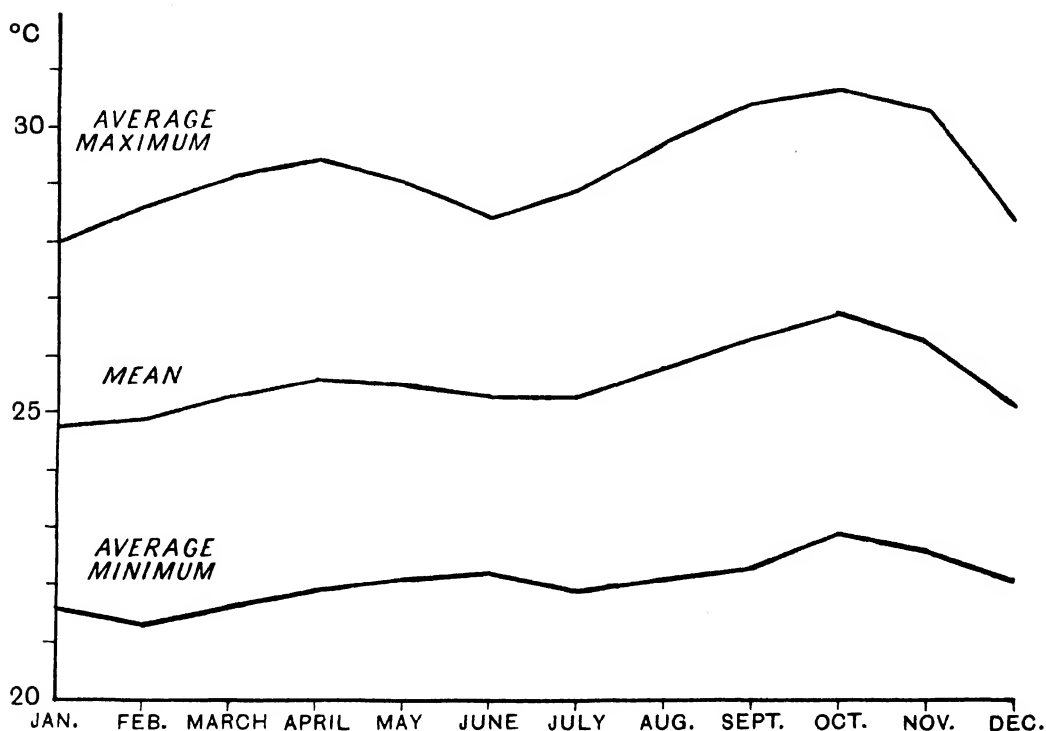
Fig. 2. Shade temperatures at H.M. Penal Settlement, River Mazaruni.
Monthly averages for the years 1920–9 inclusive.

known to fail, but occasionally (probably about once in 12 years on the average) the winter rains are so slight as to convert the two dry seasons into one very long one. This occurred in the winter of 1911–12 and again in 1925–6 and 1930–1. In such droughts, according to the accounts of observers, there is very considerable drying up of the forests. In 1925–6 a heavy mortality was noticed among *Mora Gonggrijpii* (Kleinh.) (Morabukea) seedlings, while mature trees of *Houmiri balsamifera* Aubl. (Tauroniro) were killed, presumably by drought. It is therefore likely that these droughts prevent the vegetation from being of as hygrophilous a type as is allowed by the *average* climate of the district.

In the short wet season the rain is often accompanied by squalls of wind: in the long wet season it nearly always falls vertically and with great violence.

The total rainfall of other rain forest localities in the colony is very little different from that in our district. The rainfall of rain forests in other parts of the world is often heavier, but may be considerably lower. It is seldom as evenly spread through the year. At Manáos (Amazon valley) the average total is only 165 cm. And there are three successive months with averages of less
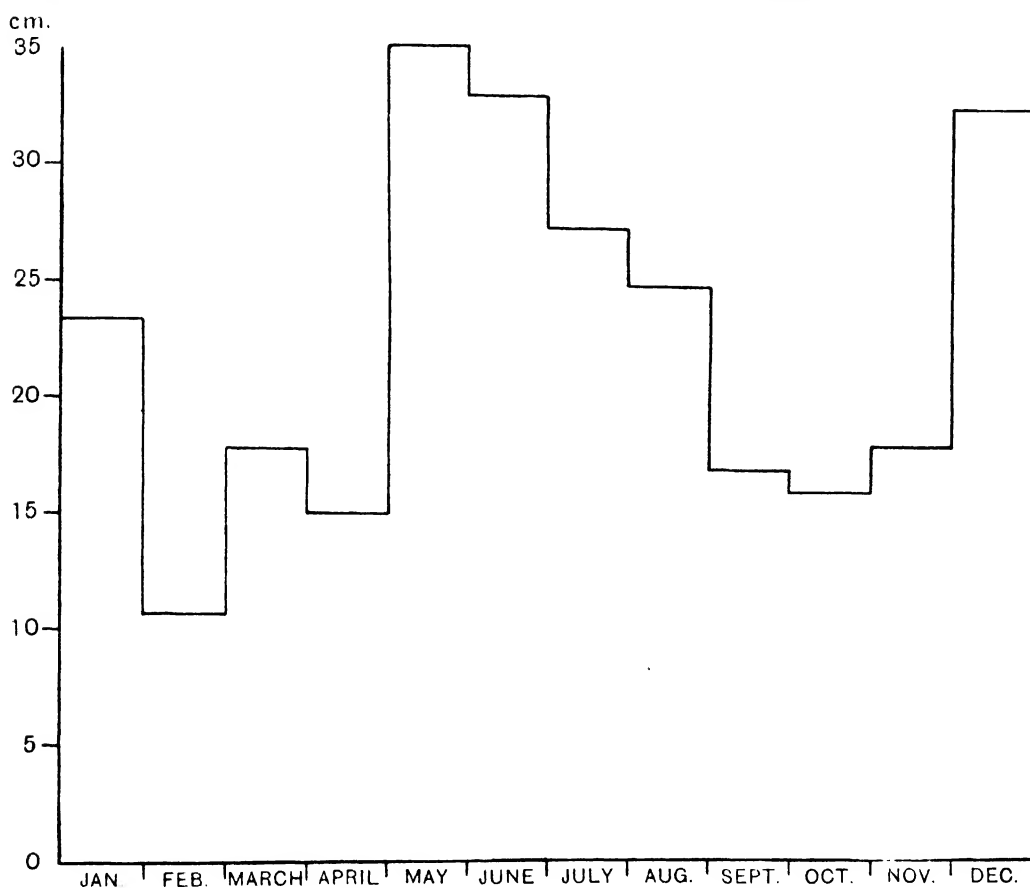
Fig. 3. Rainfall at H.M. Penal Settlement, River Mazaruni. Monthly averages for the years 1920–9 inclusive.

than 5 cm. Duala (Cameroons), with a total of 404 cm., has two successive months with less than 8 cm., the driest month having only 4·8 cm.

(c) *Wind, humidity, etc.*

The north-east trade wind blows very constantly throughout the year: at night it tends to drop and to blow less constantly from the north-east. During the dry season especially, short but violent squalls of wind are common in the afternoon, but violent winds of long duration are unknown. During any such squall several trees can usually be heard to fall: this is the normal cause

of death of old trees. According to Wood the wind is sometimes focussed on small areas, and in one place (near Bartica) "the greater part of several hundred acres of Wallaba had been blown over" (**7**, p. 8).

Thick mist and fog, according to the Indians and other observers, are rare. From our observation posts in the forest canopy (see p. 362) we often noticed light clouds lingering in the tree-tops at about 7–8 a.m.

The humidity of the air is always high—mean at 7 a.m. (1920–9) 93·7 per cent., at 1 p.m. 78·8 per cent. The lowest mean monthly humidity at 1 p.m. (near the driest time of day) during these years was 63·2 per cent. (March, 1926): this was at the end of a drought, but the humidity often falls well
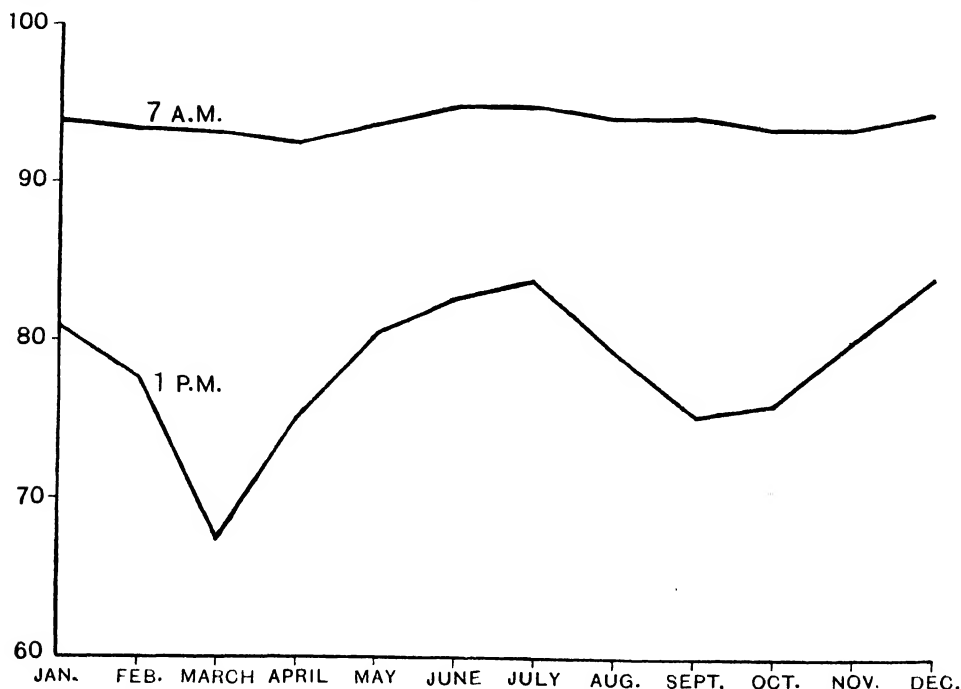
FIG. 4. Humidity at H.M. Penal Settlement, River Mazaruni. Monthly averages for the years 1920–9 inclusive.

below this figure on individual days. At night the humidity is high and varies little through the year, though in the day there are large variations according to the season. In the wet seasons the air is saturated or nearly so for long periods.

At Manáos the mean monthly relative humidity is 77 per cent. in July and 81 per cent. in January, at Duala 92 per cent. in July and 85 per cent. in January.

(*d*) *Sunshine.*

The amount of sunshine is surprisingly small. For the ten years 1920–9 the average daily amount was only 5·5 hours. During the dry seasons the monthly mean amount rises much above the yearly average (sunniest month

September with 6·3 hours per day), while during the wet seasons it falls far below it, June having an average of only 4·4 hours per day. During the dry season of 1929 we found that bright sunshine was uncommon in the afternoons and that in the mornings clouds were continually passing in front of the sun, so that it was often difficult to find times when there was bright sunshine for long enough to make light intensity measurements in the forest.

(3) *Seasonal periodicity of the vegetation.*

The climate of Moraballi Creek has a sufficiently well-marked periodici⁺y in its rainfall for some seasonal periodicity to be expected in the vegetation, in spite of the small range of temperature. The *internal* climate of the forest is very much more uniform than that of the canopy (see p. 373), so it is in the latter alone that periodicity can be expected.

The dominant species of trees are without exception evergreen, but a small proportion[1] of the subsidiary species shed their leaves partly or completely during the dry seasons (some species probably do so independently of the seasons). The species showing the best marked deciduous periods are mostly tall trees which overtop the main level of the canopy. No deciduous bush-ropes[2] or undergrowth trees were found. The dropping of the leaves is often, but by no means always, associated with flowering. The length of the bare period varies but seems always to be shorter than the length of the dry season[3].

Schomburgk (**8**, p. 258) considered that there were two well-marked flowering seasons in the year in the Guiana forest (viz. for the vegetation as a whole, not for individual species). The short rainy season, however, makes so slight a check that there is in effect a single flowering season lasting from September to March. Even at the height of the flowering season the number of trees in flower at one time is small. On the clear-felling plots (see p. 363), the felling of which lasted 19 days (in the middle of October), only 39 out of 270 trees over 5 m. high were in flower or young fruit. Flowering seasons do not exist below the main canopy. The undergrowth trees and the herbs, except some of the saprophytes, can be found in flower at any time of the year.

[1] It is a pity that we are not able to give any exact figures as to the percentage of deciduous and partly deciduous trees in our area: it seems likely that there is a complete series of types from the entirely deciduous monsoon forests to the entirely evergreen rain forests of the most hygrophytic kind. If this is so, the proportion of deciduous species would give a useful index of the position of any particular type in the series.

[2] Large woody climbers are called "bush-ropes" in the colony: this seems a better word than liane.

[3] A few examples noted in 1929 may be given:

(1) *Hymenaea Courbaril* L. (Locust). September 7th to 15th = 8 days.

(2) *Sterculia pruriens* (Aubl.) (Maho). September 9th to October 10th = 31 days.

(3) *Couratari pulchra* Sandwith (Wadara). September 15th to October 1st = 16 days.

(4) Wadara, almost bare on August 27th. Quite bare on October 1st. Buds bursting on October 9th. Young leaves expanded, but not fully green on October 17th. Another individual of this species was observed in very young leaf on October 18th and in full leaf on November 1st. Evidently in this species the bare period is fairly simultaneous in different individuals.

(4) *Biotic factors.*

The effects of man are among the most important biotic factors even in such comparatively "natural" vegetation as the Guiana rain forest.

Only a single family of Indians now lives on Moraballi Creek, but there is reason to believe that the population of the district was once greater than it is now, though it must necessarily have always been very sparse. The Indians of Guiana live by cultivating Cassava (*Manihot utilissima* Pohl.) as well as by hunting and fishing. Fields are made by clearing and burning the forest. One crop a year is obtained, and after taking two or three or exceptionally four or five crops the soil becomes exhausted, so that a new cassava field must be made. The old field may still be visited for a time to gather bananas, pineapples, etc. Each family needs about an acre (0·404 hectare). Only rarely is an old field used again after a lapse of time (probably chiefly because of the heavy labour of clearing the dense second growth), so it is clear that a considerable area of forest must have been cultivated at one time or another. Only a certain type of forest (called "*Kabiokilli*" or "field ground") on red loamy soil is used for making fields. Second growth on the site of an old field ("*mainap*") can often be recognised by the presence of certain plants cultivated by the Indians, notably bamboos (*Dendrocalamus* sp.) and certain palms.

In modern times the commercial exploitation of the forest for timber has been far more important than Indian cultivation in modifying the forest. One of the most striking features of the Guiana forest from a forester's point of view is, in Wood's words, that "in a virgin tropical forest, with several hundred species of trees all struggling for supremacy, just a few should have gained a clear dominance over the others on large areas, and that those few by good fortune, happen to be the most valuable" (7, p. 2). The only species which have so far been exploited on a large scale are Greenheart (*Ocotea Rodioei* [Schomb.]) and Wallaba (*Eperua falcata* Aubl., *E. grandiflora* [Aubl.] and *E. Jenmani* Oliv.). Greenheart is more resistant than any other known timber to the attacks of insects and marine borers and therefore fetches a high price: it is one of the colony's most valuable exports. Crabwood (*Carapa guianensis* Aubl.) and Mora (*Mora excelsa* Bth.) are also worked but on a small scale only. The rapids on the rivers have been a great obstacle to the commercial exploitation of most of the forests of the interior, especially as the Guiana timbers, like most tropical hardwoods, do not float in water.

Moraballi Creek, however, lies in the accessible region below the first falls of the Essequibo and has been worked for greenheart intermittently for at least 80 years. There were in 1929 two timber grants on the creek and in both only greenheart was cut. Greenheart occurs as a dominant (over 40 per cent. of all the trees above 16 in. [41 cm.] diameter) and also as a subordinate species in other types of forest. Forest with over 150 cu. ft. per acre

(10·5 cu. m. per hectare) of greenheart is considered commercially workable. As the pure greenheart forests do not cover a large area and are often found on ridges inaccessible from the main creek most of the greenheart working consists simply of cutting out large trees here and there, not of anything like clear felling. Though the losses are not quickly replaced, in spite of the abundance of seedlings, this has probably not affected the forest in general very much. Indeed it might be supposed that except for lessening the proportion of large greenheart trees the exploitation had no more effect than the falling of old trees in the course of nature. However, when a tree is cut down it nearly always knocks down or breaks several surrounding smaller trees (often a tree is so bound up to other trees by bush-ropes that it will not fall unless they are also cut) and a fair sized opening is formed, which may be colonised by light-demanding second-growth species, whereas when an old tree falls many of its branches have already fallen off and its wood has been softened by fungi and termites, so that it hardly damages the surrounding vegetation.

Old logs and stumps of greenheart decay extremely slowly, lasting unchanged for many years. It is therefore always possible to tell where the forest has been worked and to allow for the fact in ecological study.

In spite of all this interference, however, a great part of the forest of our area was undoubtedly in its primitive state.

During drought years epidemics of forest fires break out. There were a few small burnt patches in our area. There are no other perceptible effects of man in the forest. Of the other biotic factors it is impossible to say anything, as next to nothing is known of their effects on the vegetation. Though there are many species of herbivorous mammals, e.g. tapirs, sloths, deer, mice, the total number of individuals is so small that their effect on the vegetation is probably negligible.

III. THE STRUCTURE OF THE RAIN-FOREST COMMUNITY.

The rain forest of our area was not floristically homogeneous, but was found to consist of a regularly graded series of types, called respectively Mora, Morabukea, Mixed, Greenheart and Wallaba. The first and the last of these stand rather apart from the rest and have certain characteristics in common, above all the relatively high light intensity in the undergrowth: we therefore group them together as the *extreme* types. The other three types are very similar in most respects and the light intensity in the undergrowth is low in all of them: these we call the *central* types.

In Part II the characteristics of these types will be described and their relation to edaphic factors will be pointed out. Since, however, the five types are very similar in structure, a description can be given of the strata and other synusiae (i.e. groups of plants occupying approximately the same " niche ")

composing the forest community which will apply to all of them. A first analysis may be made into:

(1) Plants not dependent on others for mechanical support (trees, shrubs and herbs), (*a*) autotrophic, (*b*) heterotrophic.

(2) Climbing plants.

(3) Epiphytes, (*a*) autotrophic, (*b*) heterotrophic.

The first group can be divided into a number of strata, the others less easily. It is clear that the structure of the community depends mainly on competition for light and that the three groups just distinguished are merely three different ways of solving the light problem.

(1) *Stratification of trees, shrubs and herbs.*

It is at once evident on entering the forest that there is a small herb stratum and a tall herb and shrub stratum, but how many tree strata there are is not easily decided by observation from the ground, owing to the great density of the vegetation. Most observers of tropical forests have spoken of a large number of strata of trees; thus Chipp (**9**, p. 207) says that in the African rain forest "the canopy consists of three strata or tiers, whilst a fourth and lowest stratum includes the smallest trees and biggest shrubs," and Benoist(**10**) in the forests of French Guiana recognises, (i) a stratum of trees 30–40 m. high, (ii) an "*étage dominé*" of trees 10–25 m. high, (iii) a stratum of "*arbustes*" a few metres high. Our preliminary observations on the forests of our area showed that there was a distinct undergrowth stratum of small trees probably corresponding to Chipp's lowest stratum and Benoist's "arbustes" and there was also a main canopy at about 30 m. It was thought that more intensive study might resolve the latter into two or more strata and that other strata might be discovered between the small tree stratum and the canopy.

The first method tried was climbing tall trees. From the observation posts established by the zoological members of the expedition it was possible to look down on large areas of the canopy from exceptionally tall trees. Pl. XXII, phot. 1 shows the appearance of the canopy from an observation post at 110 ft. (33·6 m.) in forest of the mixed type. The following is a copy of field notes on the view from this point made at the time: "There is no definite flat-topped canopy: there are two more or less clear [upper] layers, but they are both discontinuous, so the general effect is very uneven. Any two tall trees may be separated from one another by one or more lower trees. The lower trees do not grow under and are not much overshadowed by the higher. Practically all the lower trees of the canopy are covered and bound together with lianes. Apart from the ordinary upper canopy trees there are rare ones which tower far above all others. Two such outstanding trees were seen [one of these can be seen in Pl. XXII, phot. 1] whose whole crowns were well clear of all the surrounding trees." There was no sign of a stratum between the canopy and the clearly marked layer of small trees about 5–9 m. high.

Further information about the stratification was obtained by clear felling a number of plots of forest and measuring all the trees on them. Two plots 200 × 25 ft. (61 × 7·6 m.) and one 400 × 25 ft. (122 × 7·6 m.) in forest of the Mixed type were felled.

The plots were marked out with cords with the help of a prismatic compass. On the two smaller plots all undergrowth less than 15 ft. (4·6 m.) was then cleared away and on the large one all less than 40 ft. (12·2 m.). Next the smaller trees were cut down with a cutlass and measured. Finally the big trees were felled with an axe in a carefully selected order so that the larger ones should not crush the smaller in falling. A good deal of trouble was caused by bush-ropes which often prevented a tree from falling when it was cut right through and it was sometimes necessary to fell a tree outside the plot which was holding up others. The height of the lower limit of the crown of each tree (i.e. the lowest leaves, neglecting stray twigs) was measured, as well as the total height, and the vernacular name of the species was obtained from the Indian wood-cutter. The flowers or fruit when present were collected and notes were made on the epiphytes and bush-ropes.

The measurements for the three plots are given in Table I.

Table I. *Trees on clear-felling plots (Mixed forest).*

The clear-felling plots formed part of the sample plot of Mixed forest and identifications of the vernacular names will therefore be found in Table X (Part II).

* = in flower or young fruit.

Plot 1 (200 × 25 ft. = c. 61 × 7·6 m.). All trees over 15 ft. (4·6 m.) high measured.

(a) Trees of species which when mature are usually over 90 ft. (27 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Assipoko	62	95	Kakaralli, smooth leaved*	36	65
Assipokoballi, broad leaved	13	16	,, ,,	9	17
,, ,,	15	27	,, ,,	9	16
Bahurada, Sandhill	7	18	,, ,,	29	59
,, ,,	6	18	Karahoro	99	112
Baromalli	26	56	Kauta	19	36
,,	15	16	,,	18	28
,,	53	91	,,	12	34
,,	16	18	,,	13	16
,,	45	25	,,	13	23
Determa	61	106	Kautaballi	47	60
Greenheart	22	77	,,	32	63
,,	15	38	,,	15	19
,,	55	107	,,	11	17
,,	17	26	,,	28	37
,,	29	68	,, *	44	90
,,	11	19	,,	32	60
,,	14	31	,,	20	23
,,	22	38	,, *	63	92
,,	19	54	,, *	30	106
,,	13	44	Keriti	12	22
Kairima	13	22	Marishiballi	17	29
Kakaralli, common	35	68	,,	14	26
,, ,,	14	27	Silverballi, Buradie	18	35
,, ,, *	60	92	,, ,,	11	18
,, ,, *	80	106	Ulu	11	20
,, ,,	21	31			

Plot 1 (*contd.*).

(*b*) Trees of species which when mature are usually 60–90 ft. (18–27 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Aiamorakushi	56	82	Kairiballi	12	22
Arara*	40	76	,,	16	22
,, *	45	70	,,	14	21
,,	11	16	,, *	57	92
,,	13	16	,,	8	18
Awassakuli, big kind	33	41	,,	12	25
,, ,,	10	17	Kirikowa	10	18
Baniaballi	16	31	,,	19	21
Kairiballi	16	30	Kokoritiballi	12	21
,,	42	66	Kulashiri, big kind*	34	41
,,	13	18	Trisyl	20	50
,,	20	31	,, *	57	83
,,	20	35	,,	11	18
,,	9	21			

(*c*) Trees of species which when mature are usually under 60 ft. (18 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Buri	9	20	Yarri-yarri, fine leaved	6	18
,,	11	16	,, ,,	9	19
,,	8	19	,, ,,	6	20
Kumaramara, broad leaved	22	38	,, ,,	7	26
Okokonshi, fine leaved	7	16	,, ,,	4	20
,, ,,	11	19	,, ,,	9	30
,, ,,	11	20	,, ,,	4	15
,, ,,	15	30	(Unknown "B")	17	31
Yarri-yarri, fine leaved	6	27			

(*d*) Trees of species whose usual mature height is unknown.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
(Unknown: like Kuyama)	26	38	(Unknown)	24	39
(Unknown)	20	23	(Unknown)	13	18
(Unknown)	72	89			

Plot 2 (200 × 25 ft. = *c.* 61 × 7·6 m.). All trees over 15 ft. (4·6 m.) high measured.

(*a*) Trees of species which when mature are usually over 90 ft. (27 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Arumatta	36	80	Kauta	16	24
Baradan	36	39	,,	16	29
,,	88	119	,, ?	7	20
Baromalli	18	18	,,	47	72
,,	11	17	,,	67	95
Duru*	79	101	,,	26	46
Fukadi, broad leaved	27	*c.* 50	Kautaballi	6	23
Greenheart	23	41	,,	18	29
,,	32	56	,,	10	18
,,	23	45	,,	12	21
,,	8	21	,,	32	52
,,	10	22	Kurokai	12	23
,,	14	26	Maho, fine leaved	25	25
Hiowaballi	27	56	,, ,,	30	30
Kakaralli, common	10	18	,, ,,	46	46
,, ,, *	58	101	,, ,,	43	49
,, ,, *	88	124	Manniballi	20	24
,, ,,	42	56	Marishiballi	12	18
,, smooth leaved	8	22	,,	24	39
,, ,,	13	21	,,	28	33
,, ,,	23	42	,,	44	72
,, ,,	6	18	Shibadan	17	26
,, ,,	6	19	Silverballi, Gingergale	25	31
,, ,,	43	116	,, broad leaved white	12	18
,, ,,	45	91	,, ,,	46	65
,, ,,	66	103	Suradan	38	49
Karahoro	63	67	Wadara	63	85

Plot 2 (*contd.*).

(*b*) Trees of species which when mature are usually 60–90 ft. (18–27 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Arara	—	35	Okokonshi, broad leaved	18	23
,,	28	53	,, ,,	23	32
,,	20	27	,, ,,	71	82
Kairiballi	38	45	Table Tree*	—	98
,,	13	18	,, *	68	81
,,	11	16	,, *	69	87
,,	10	17	Trisyl	15	32
Kakaralli, fine leaved	6	19	,,	13	21
,, ,,	16	29	,,	20	23
,, ,,	7	20	,,	12	26
Kulashiri, common	20	20	,,	21	26
,, ,,	29	34	Warakusa	19	39
Okokonshi, broad leaved	15	27			

(*c*) Trees of species which when mature are usually under 60 ft. (18 m.) high.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Adebero	16	26	Okokonshi, fine leaved	6	18
,,	13	19	,, ,,	9	22
,,	10	16	,, ,,	6	18
,,	4	15	,, ,,	12	22
Akarako	10	17	,, ,,	14	24
Buri	18	29	,, ,,	7	20
,,	9	16	,, ,,	6	17
Kurihikoyoko*	7	19	,, ,,	27	36
,, *	6	17	Palm, blow-pipe	26	26
,, *	8	17		(three shoots)	
,, *	7	18	Unknown "A"	7	16
Okokonshi, fine leaved	6	20	,,	11	28
,, ,,	27	54	,,	10	29
,, ,,	11	21	,,	11	24

(*d*) Trees of species whose usual mature height is unknown.

Native name	Height of first leaves ft.	Total height ft.	Native name	Height of first leaves ft.	Total height ft.
Awassakuli (unknown kind)*	24	33	Unknown (like Suradan)	28	32
Unknown (like Suradan)	23	23	Unknown	35	55
,, ,,	25	29			

Plot 3 (400 × 25 ft. =*c.* 122 × 7·6 m.). All trees over 40 ft. (12·2 m.) high measured.

(*a*) Trees of species which when mature are usually over 90 ft. (27 m.) high.

Native name	Total height ft.	Native name	Total height ft.
Assipoko	49	Kauta	68
Baradan	136	Kautaballi	68
Greenheart	44	,, *	71
Kairima	56	,, *	102
Kakaralli, common*	83	,,	80
,, ,, *	96	,,	87
,, ,,	91	,,	43
,, ,,	66	,,	71
,, ,,	118	,, *	84
,, smooth leaved	49	Maho, fine leaved	62
,, ,, *	85	Manniballi	89
,, ,, *	94	,, *	131
,, ,, *	79	Marishiballi	42
,, ,, *	74	Shibadan	112
,, ,,	61	,,	64
Kauta	86	Shirua	79
,,	60	Silverballi, Kurahara	80
,,	108	Yaruru*	137
,,	100	,,	60

24-2

Plot 3 (*contd.*).

(*b*) Trees of species which when mature are usually 60–90 ft. (18–27 m.) high.

Native name	Total height ft.	Native name	Total height ft.
Arara*	60	Kirikowa*	71
,,	54	Trisyl	58
Baniaballi	76	,,	50
,,	80	,, *	89
Barabara*	79	,, *	82
Kairiballi	65	Turu (Palm)*	86
,,	52	,, ,, *	84
,,	55	Warakusa	c. 53
,,	87		

(*c*) Trees of species which when mature are usually under 60 ft. (18 m.) high.

Unknown "A"*   48

(*d*) Trees of species whose usual mature height is unknown.

Unknown (like Assipokoballi)*   103

The heights were first plotted in height-intervals of 1 ft. (the original measurements having been made in feet): later they were grouped into height-intervals of 10 ft. In either case a curve of similar type is obtained. Table II gives the results in the second form and in Fig. 5 the same results are expressed graphically. Other data are given in Tables III and IV.

Table II. *Total heights of trees on the clear-felling plots grouped in intervals of 10 ft.*

Totals for two plots each 200×25 ft. (*c.* 61×7.6 m.) and one 400×25 ft. (*c.* 122×7.6 m.). On the two small plots all trees over 15 ft. (4·6 m.) were measured: on the large plot (half the total area) only trees over 40 ft. (12·2 m.) were measured, so in the "16–25," "26–35" and "36–45" height-intervals the totals have been doubled, while the three trees on the large plot between 40 and 46 ft. have been left out.

	Number of individuals of species whose usual mature height is				
Height ft.	Under 60 ft. (18 m.)	60–90 ft. (18–27 m.)	Over 90 ft. (27 m.)	Unknown	Total
16– 25	62	46	74	6	188
26– 35	24	26	34	6	90
36– 45	4	8	20	4	36
46– 55	2	7	9	1	19
56– 65	0	3	16	0	19
66– 75	0	3	11	0	14
76– 85	0	10	10	0	20
86– 95	0	5	12	1	18
96–105	0	1	6	1	8
106–115	0	0	7	0	7
116–125	0	0	4	0	4
126–135	0	0	1	0	1
136–145	0	0	2	0	2

N.B. Since the original measurements are given to the nearest foot, e.g. 17 ft. 9 in. and 17 ft. 6 in. both counting as 18 ft., the height-intervals "16–25 ft." includes heights between 15 ft. 6 in. and 25 ft. 5 in. The smallest height-interval therefore has to be "16–25 ft.," not "15–24 ft.," as trees between 14 ft. 6 in. and 15 ft. were not measured.

The curve for the total heights shows that there is a well-marked undergrowth stratum, ending rather abruptly above at about 45 ft. (14 m.). The greatest number of individuals in the main canopy comes in the 76–85 ft.

(23·2–25·9 m.) height-interval. Above 95 ft. (29 m.) the curve falls off steeply, representing the relatively few but very large trees of the upper part of the main canopy. There are some indications of a maximum on the curve in the 56–65 ft. height-interval, but it is probably not significant. The curve for the heights of the first leaves shows that the lower limit of the main canopy is in the 56–65 ft. (17–19·8 m.) height-interval.
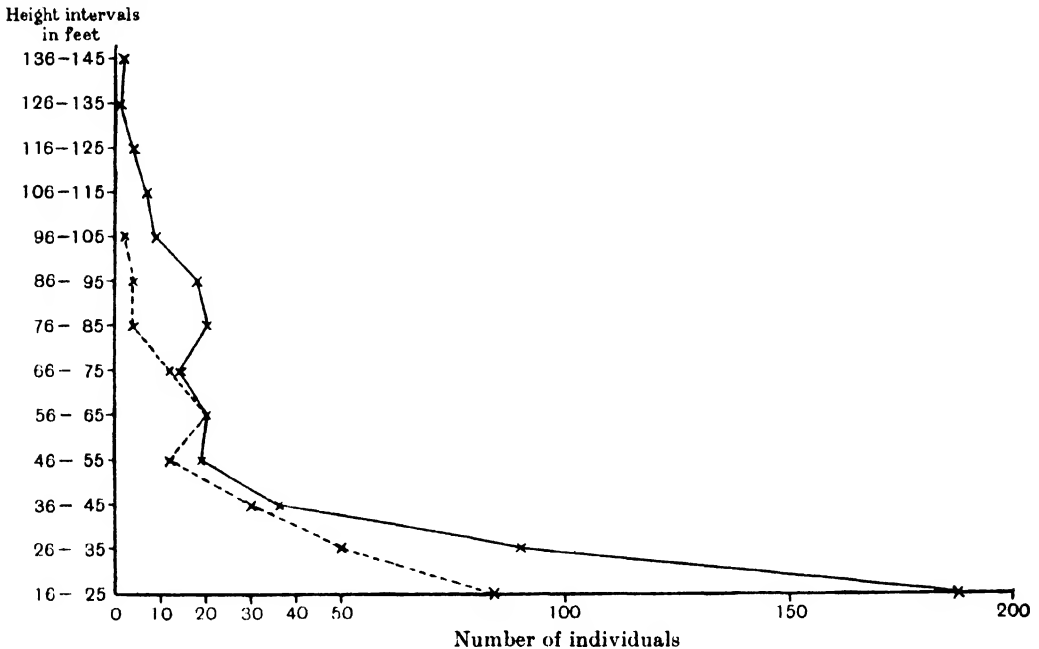
FIG. 5. Total heights and heights of first leaves of trees on clear-felling plots. The continuous line represents distribution of total heights among the height intervals, using figures in last column of Table II. The broken line represents distribution of heights of first leaves. To obtain the curve the figures in last column of Table III have been multiplied by 2.

Table III. *Heights of first leaves of trees on the clear-felling plots grouped in intervals of 10 ft.*

Measurements were made to the first leaves of the crown, neglecting leaves on stray twigs.

Totals for two plots each 200 × 25 ft. (*c.* 61 × 7·6 m.). The height of the first leaves was measured on all trees over 15 ft. (4·6 m.) high, except on two which were damaged in felling.

| Height ft. | Number of individuals of species whose usual mature height is | | | | |
	Under 60 ft. (18 m.)	60–90 ft. (18–27 m.)	Over 90 ft. (27 m.)	Unknown	Total
Under 16	37	21	28	1	87
16– 25	4	15	23	5	47
26– 35	3	4	15	3	25
36– 45	0	4	11	0	15
46– 55	0	0	6	0	6
56– 65	0	3	7	0	10
66– 75	0	3	2	1	6
76– 85	0	0	2	0	2
86– 95	0	0	2	0	2
96–105	0	0	1	0	1
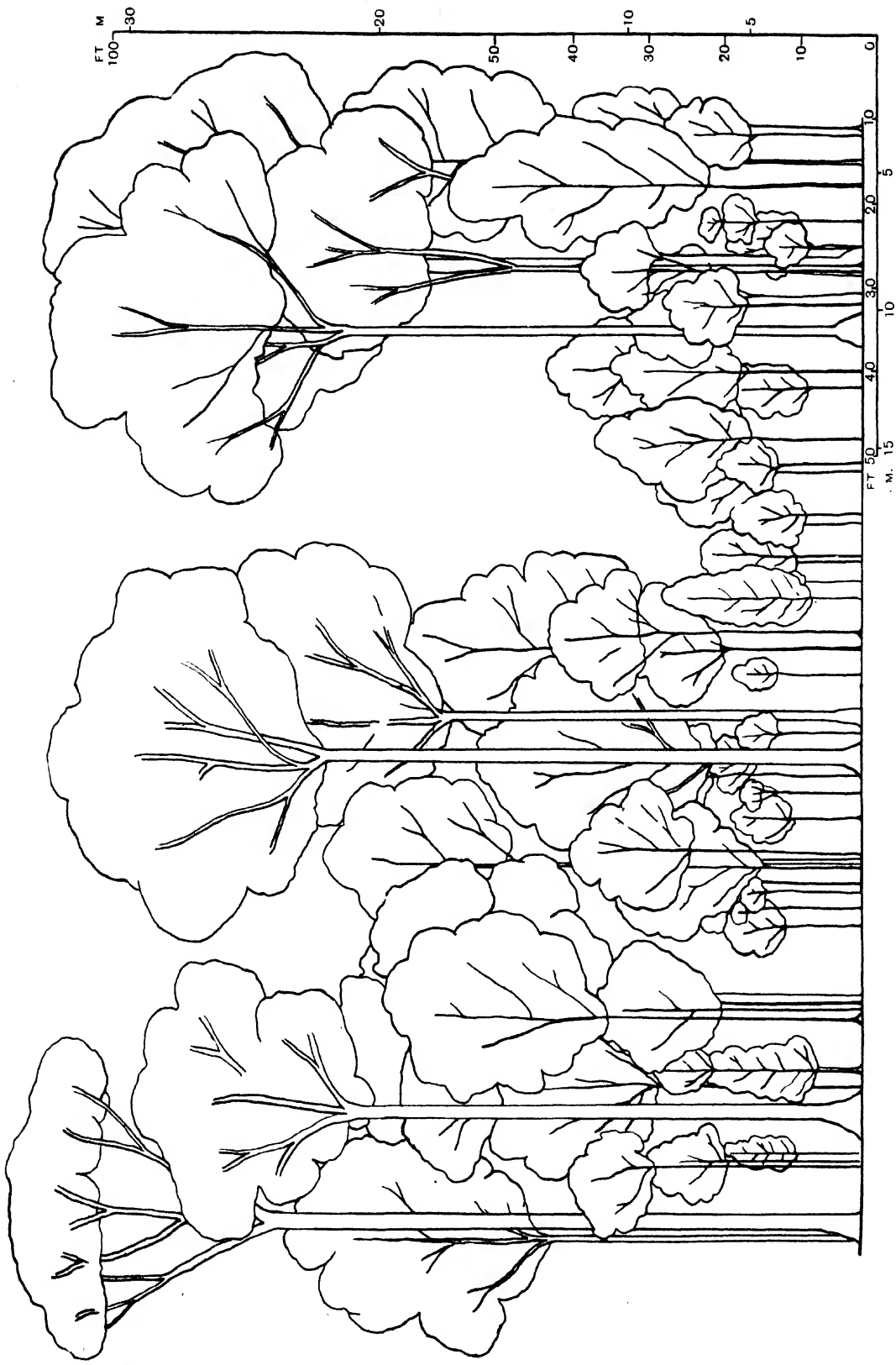
Table IV. *Numbers of trees in flower or young fruit on the clear-felling plots grouped in height-intervals of 10 ft.*

Totals for two plots each 200 × 25 ft. (c. 61 × 7·6 m.) and one 400 × 25 ft. (c. 122 × 7·6 m.). On the two small plots all trees over 15 ft. (4·6 m.) were measured: on the large plot (half the total area) only trees over 40 ft. (12·2 m.) were measured, so in the "16–25," "26–35" and "36–45" height-intervals the totals have been doubled. The three trees on the large plot between 40 and 46 ft. (none of which was in flower) have been left out.

| Height ft. | Number of individuals in flower or young fruit of species whose usual mature height is | | | | | Total as % of total number of trees in height-interval |
	Under 60 ft. (18 m.)	60–90 ft. (18–27 m.)	Over 90 ft. (27 m.)	Unknown	Total	
16– 25	8	0	0	0	8	5
26– 35	0	0	0	2	2	2
36– 45	0	2	0	0	2	6
46– 55	1	0	0	0	1	5
56– 65	0	1	1	0	2	10
66– 75	0	2	2	0	4	29
76– 85	0	6	4	0	10	50
86– 95	0	4	4	0	8	44
96–105	0	1	4	1	6	75
106–115	0	2	0	0	2	29
116–125	0	1	0	0	1	25
126–135	0	0	1	0	1	100
136–145	0	0	1	0	1	50

There is thus very little evidence for the existence of a stratum between the undergrowth and the main canopy.

The analysis of trees in each of the height-intervals into groups according to their usual mature size shows several interesting facts. Only about a third of the trees in the undergrowth stratum belong to species which spend all their lives at that level, the majority are young individuals of canopy species. Though the majority of the undergrowth species do not reach a greater height than 35 ft. (10·7 m.), exceptional individuals may reach the 46–55 ft. (14–17·8 m.) class. The species of the 60–90 ft. (18–27 m.) group reach their second maximum of numbers at 76–85 ft. (23·2–25·9 m.), but here again exceptional individuals may reach greater heights. The "over 90 ft. (27 m.)" group are rather irregularly distributed in the upper height-intervals. Both the 60–90 ft. and the "over 90 ft." groups have a fairly well-marked minimum of numbers in the region between the undergrowth level and the canopy, suggesting that once a tree gets clear of the undergrowth it grows relatively rapidly up to the canopy. It is clear, however, that the stratification is very irregular and ill-marked, as can also be seen from the diagrammatic profile in Fig. 6.

The figures for the numbers of trees in flower, though small, show one or two facts relevant to the question of stratification. There are two distinct flowery layers, separated by a well-marked flowerless region. The species of

Fig. 6. Diagrammatic profile of a strip 135 ft. (41 m.) long and 25 ft. (7·6 m.) deep on a clear-felling plot (Mixed forest). A few trees are completely hidden from view by others standing in front of them. The positions, total heights, heights of the lowest branches and lowest leaves, and the diameters at breast height are based on actual measurements.

the "under 60 ft." group flower when in the smallest height-interval (16–25 ft.) and form the lower layer. The maximum flowering region in the canopy is the 76–85 ft. (23·2–25·9 m.) height-interval, which is the region of the maximum number of individuals. When the numbers of trees in flower are expressed as a percentage of the total number of individuals in each height-interval, a striking result is obtained. The percentages show a sudden sharp increase at the 56–65 ft. (17–19·8 m.) height-interval, i.e. at the lower limit of the canopy, and the percentage remains uniformly large above that height. The low percentages in the lower layers are no doubt due to the preponderance of young trees there and also to the fact, already referred to (p. 359), that the undergrowth species flower continuously and have no well-marked flowering season, so that the number of individuals in flower at any one time is always bound to be small.

We can therefore describe the stratification of the trees and shrubs as follows:

There is a canopy of trees averaging about 24 m. high. Out of this general level many trees raise themselves[1] incompletely to heights of up tc 42 m., that is, though the upper part of the crown is raised far above its neighbours, the lower part is not separated by a space from the general mass of foliage. These taller trees have a tendency to grow together in groups[2], which was noticed many times in forest of all types (see Fig. 6). As there is no discontinuity separating the taller from the lower trees of the canopy they cannot be considered distinct strata, though a floristic division can be made into species rarely exceeding 27 m. and species commonly taller than 27 m.

Besides these very tall trees there are *outstanding trees* whose whole crown is lifted clear of all its neighbours. Such trees are sparingly spread through the forest (probably never more frequent on the average than 1 per sq. km.). The average height of such trees is about 43 m. The highest three measured by us were *Couratari pulchra* Sandwith (Wadara), 43·1 m., *Terminalia Tanibouca* Rich. (Fukadi), 44·9 m. and *Mora Gonggrijpii* (Kleinhoonte) (Morabukea), 43·6 m., but we saw trees which were probably higher and good authorities state that trees up to 60 m. are known in Guiana. Our measurements are of the same order as those of Spruce who says the highest tree measured by him in the whole of his travels on the Amazon was 47·9 m.[3] (**11**, vol. **1**, p. 18). These outstanding trees belong to peculiar species, which are rarely found in the main canopy (the Morabukea quoted above is an

[1] It is likely that in forest types with single dominant species the canopy is very much more even than in the mixed forest of the clear-felling plots.

[2] The explanation of this phenomenon which was suggested in the field was that these groups represent holes in the canopy made by the death of a very large old tree which has stimulated the growth of the surrounding trees.

[3] This figure is also of the same order as those given by **Schlich** (**12**) for the extreme heights of deciduous trees in Europe.

Phot. R. W. G. Hingston.

Phot. 1. The canopy (Mixed and Morabukea forest) seen from an observation post at about 34 m. On the horizon at the extreme right an "outstanding" tree can be seen.

Phot. J. E. Duffield.

Phot. 2. Undergrowth of Mora forest. The buttressed tree is *Mora excelsa* Bth, belonging to upper part of canopy. Note habit of small tree to the right (*Duguetia* sp.) which is characteristic of trees of the undergrowth stratum.

DAVIS AND RICHARDS—MORABALLI CREEK
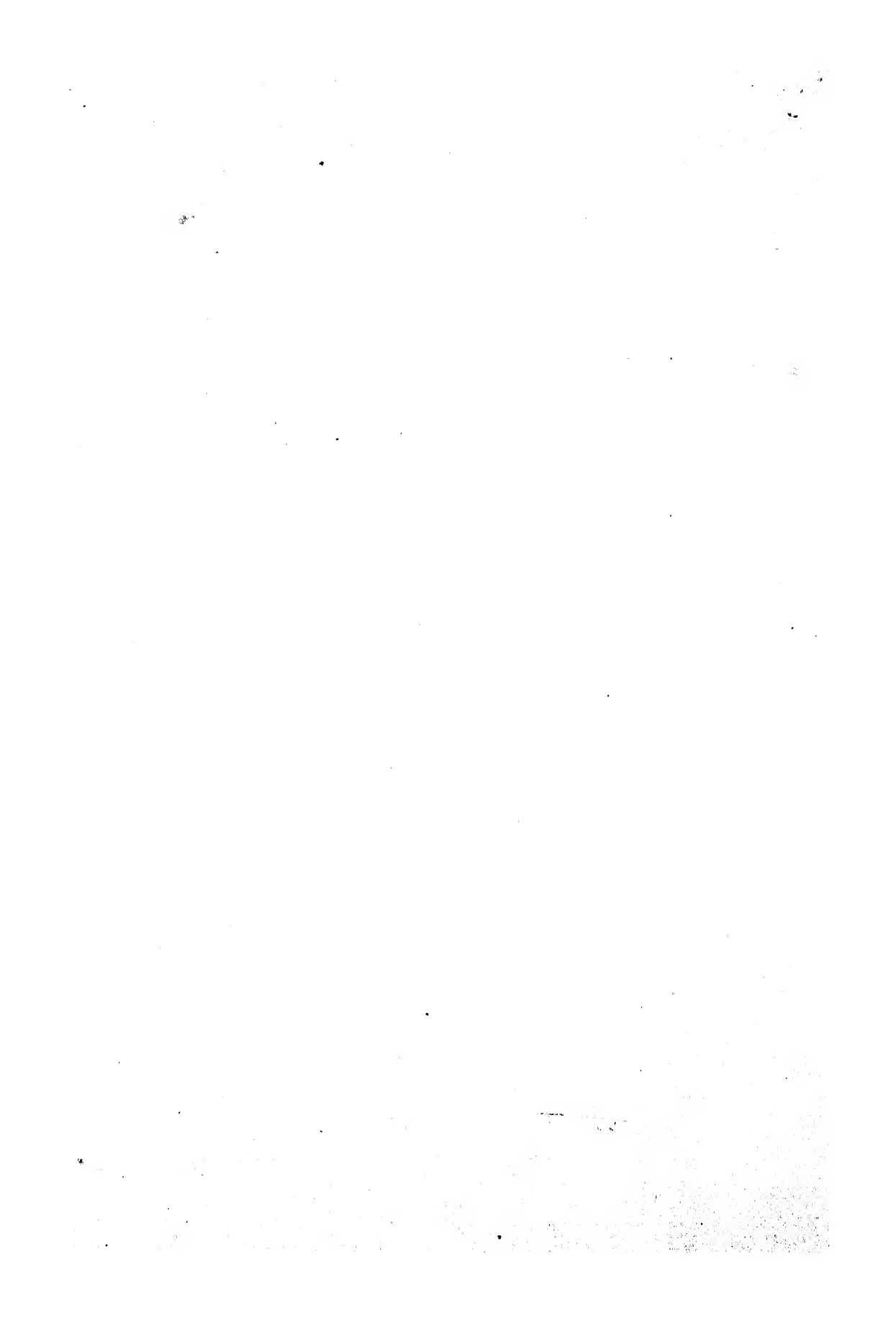
exception), the commonest being *Couratari pulchra* Sandwith (Wadara), *Hymenaea Courbaril* L. (Locust), *Mimusops* sp. (Balata), *Peltogyne pubescens* Bth. (Purpleheart)[1] and *Bombax* spp. (Silk Cotton).

Buttressing is a common feature among outstanding and canopy trees.

There is a well-marked *undergrowth stratum* of trees up to about 14 m. high. About half the trees in this layer are young individuals of canopy species, but the proportion of true undergrowth species to young canopy species varies in different types of forest. Among the true undergrowth trees the family Annonaceae is by far the most important (*Duguetia* and *Anaxagorea* spp. etc.), but the habit of all of them, whether young individuals of canopy species, Annonaceous or other true undergrowth species is very uniform and characteristic. The conical shape and numerous short horizontal branches are shown well in Pl. XXII, phot. 2 and in Fig. 6, though a few species (e.g. *Psychotria* spp.) have a more spreading form.

None of the true undergrowth tree species are buttressed, but young specimens of canopy species often develop buttresses before reaching the canopy. The whole question of buttressing will be discussed in Part II.

Between the canopy and the undergrowth strata is a region occupied only by immature trees on their way up to the canopy and by exceptionally tall individuals of undergrowth species which stand out above the undergrowth stratum much as Purplehearts and Wadaras stand out above the canopy.

The red or nearly colourless, limply hanging type of young leaf is a feature of the woody plants of the forest at all levels equally. It is not confined to the undergrowth.

Below the lowest tree stratum two ill-defined layers of small undergrowth may be distinguished[2]:

(i) A layer of small shrubs and tall herbs whose average height is a little over 1 m. To this belong some small palms (*Bactris simplicifrons* Mart. and other species), *Cephaelis violacea* (Aubl.), several abundant species of Marantaceae and various large ferns such as *Amphidesmium rostratum* (H.B.K.) and some small tree-ferns, but nearly always it consists mainly of small tree saplings. It is a characteristic of the Morabukea type of forest that this layer consists of a dense level growth of saplings of the dominant canopy tree species excluding almost everything else.

(ii) A layer of tree seedlings and small herbs up to about 40 cm. high. Here again the true inhabitants of this layer are mostly scattered and form an insignificant proportion of the total bulk of vegetation. Seedlings of the

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[1] This remarkable tree was rare at Moraballi, probably because it had been cut out by the Indians who value its bark highly for making "wood-skin" canoes. Our Indians told us that at Tapakuma Lake on the Pomeroon River, where Purpleheart is abundant, the trees stand out above the forest "like umbrellas."

[2] In some types of forest (notably in the Mora type) two layers are hardly distinguishable.

dominant canopy tree species are exceedingly abundant in all the drier types of forest and occasionally form a layer of closed vegetation. Among the true herbs three societies may be recognised.

(a) *Society of green flowering herbs*, whose abundance is proportional to the amount of light penetrating through the upper layers. Most of the constituent species have a good tolerance of exposure to strong light and immediately become very abundant wherever the canopy is temporarily removed as in the openings made by felling large trees. In the greater part of the forest, especially the three central types (see p. 361) where the shade on the floor is intense this society is completely lacking. Many of its members show a strongly marked social habit (especially *Leandra divaricata* [Naud.] which spreads by stolons and forms dense patches much like *Circaea lutetiana* L. in an English wood). All the grasses of our area, excepting one tall species (*Olyra micrantha* H.B.K.), belong to this society, but they are not abundant enough to be conspicuous[1].

(b) *Society of saprophytes*. This society differs from the last in being apparently shade loving (being confined to the shadiest spots of the forest floor) not light loving. It occurs in scattered patches where the dead-leaf layer is thick (usually only when it is over 4 cm. thick). The conditions for its existence (i.e. shade and abundant humus) are only found at all regularly in the " central" types of forest (above all in the Morabukea type), but isolated individuals of certain members live in the "extreme" types and in parts of the "central" types where the society as such does not occur. The constituent species are various Burmanniaceae, Gentianaceae and one orchid, *Wullschlaegelia calcarata* Bth.[2] The only green plant is a small fern, *Schizaea fluminensis* Miers, which must almost certainly be largely saprophytic, as in spite of the fact that the lamina is under 4 mm. wide and 3 cm. long (the height is about 2–3 dm.), it habitually lives in the most intense shade. It is always found on thick humus associated with colourless saprophytes: it is tuberous. One parasitic herb, *Helosis cayennensis* (Swartz) (Balanophoraceae) occurred, though very rarely, in our area.

(c) *Society of ferns*. This is intermediate between (a) and (b) in its demands, since many of its members cannot stand exposure to direct sunlight (other than sun-flecks) and it is more shade tolerant than (a) though less so than (b). It is the most extensive of the ground societies in the central types of forest but poorly developed in the extreme types.

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[1] A possible explanation of the scarcity of grasses in the undergrowth of tropical rain forests is the extreme stillness of the air, which may make wind pollination uncertain. It is perhaps significant that one of the forest grasses, *Pariana radiciflora* Sagot ex Doell. was observed by us to be habitually visited by insects (*Melipona* spp. and Phorid flies). The flowers have ten stamens with large yellow anthers so that the spikes are very conspicuous.

[2] Some of the other ground orchids though green may be hemi-saprophytes and really belong to this society; they tolerate fairly deep shade.

(2) *Stratification of climate within the forest.*

Having described in detail the stratification of the plants which are not dependent on others for mechanical support, some idea should now be given of the internal climate determined by the vegetation itself and of its stratification. The stratification of the plants which are dependent on others for support will be described afterwards, since it is quite clearly mainly determined by the stratification of the internal climate: thus the stratification of the "independent" plants is a response to the general climate of the region, while that of the climbers and epiphytes is mainly a response to the stratification of climate produced by the other members of the community.

It is not possible to give here a quantitative description of the internal climate of the rain forest of our area as we did not make regular meteorological observations, but Allee (**13**) and McLean (**14**) obtained some data for the rain forests of Panama and South Brazil respectively and many of their conclusions doubtless apply equally to our area. A few points may however be emphasised here.

The most striking feature of the internal climate is the extraordinary constancy of physical conditions in the lower layers of the forest. As Allee says: "The animals of the lower forest...would need only to avoid the higher temperature, light intensity and lower humidity of the sun flecks in order to keep under conditions so constant that they must excite the envy of every experimental ecologist with experience in trying to control environmental factors for land animals in a laboratory" (**13**, p. 299). This uniformity of conditions diminishes upwards, till in the upper part of the canopy it is no greater than that of the general climate of the region, which, though it shows little seasonal change, has relatively sharp differences between day and night. The diminution of uniformity with height above the ground is not constant, but according to McLean (and this must be true of our forests also) changes sharply as soon as the stratum of undergrowth trees is passed.

The factors which are most strikingly different in the internal and general climates are temperature, wind, humidity and light. *Temperature* shows much smaller day and night variations in the forest undergrowth than in the upper layers and outside. *Wind* shows one of the most striking gradients. In the canopy a gentle wind blows almost continuously, at least during the day, so that flexible leaves are always moving: in the undergrowth the air is normally so still that smoke rises quite vertically and loose scraps of paper are never moved. Squalls such as often blow for a few seconds before rain may penetrate deeply enough into the forest to cause leaves in the undergrowth to stir. During a spell of dry sunny weather in October, 1929, there was such a strong wind that on several mornings leaves near the ground were kept in motion for several hours on end. Such breezes in the undergrowth have a marked drying effect on the mosses and epiphyllae. Some measurements were made which

give some idea of the gradients of temperature and *humidity* (Table V). The two trees from which observations were made were partly cleared of bush-ropes so the values are probably abnormally low.

No measurements were made of the *light* gradient, but some values can be found in Allee's paper (**13**). The light intensity near the ground varies widely according to the forest type, as will be shown later, but it is important to notice that even in the shadiest type of forest numerous sun-flecks reach the forest floor.

A mature forest tree will therefore live under conditions very widely different from those it lived under when it was young and it is not surprising that in some forest types species which may be very abundant as young plants are quite absent as mature individuals, e.g. *Jessenia oligocarpa* Griseb. et H. Wendl (Turu Palm) in Wallaba forest.

(3) *Stratification of climbers.*

Under the heading of climbers we here include some plants whose primary roots do not reach the ground, but since their mature growth-form closely resembles that of the true climbers they belong to the same ecological group. All such plants are included under the local name of "bush-rope."

The climbers are stratified into three layers:

(a) *Climbers reaching the canopy.* These climb over even the tallest trees (often to over 40 m. from the ground) of the main canopy, but were not observed on outstanding trees. They bear few or no leaves below the canopy. Three chief groups can be recognised, but they differ morphologically more than in their general relations to the environment: (i) Typical lianes, most of which are twiners, having massive woody stems, e.g. *Bauhinia* spp., *Strychnos* spp., *Dioclea glabra* Bth., *Arrabidea candicans* Rich. and many other Bignoniaceae: *Marcgravia* spp. and *Souroubea guianensis* Aubl. are exceptional in attaching themselves by aerial roots. (ii) Root climbers with slender stems. The very abundant species *Schlegelia violacea* (Aubl.) and some Araceae are included: most of this group do not reach higher than the crowns of the lower trees in the canopy, but *Schlegelia* was twice noted climbing to 42 m. (iii) Epiphytic trees and shrubs sending massive aerial roots to the ground. To this group belong *Clusia* of which several species were very abundant in most types of forest, *Coussapoa fagifolia* Klotzsch and *Ficus* spp.

(b) *Climbers on undergrowth trees* and on the lower part of canopy trees. All of these are more or less herbaceous, e.g. *Lygodium micans* Sturm., *Salpichlaena Hookeriana* (O. Ktze.), *Carludovica coronata* Gleason, *Smilax* spp., *Desmoncus* sp. (a scrambling palm).

(c) *Small herbaceous climbers* never reaching a greater height than 3 m., e.g. *Trichomanes pedicellatum* Desv.

The climbers of the canopy, especially the *Clusia* group, are serious competitors with the trees for light. A large *Clusia* often occupies at least half the space that would otherwise be occupied by the crown of the tree to which

Table V. *Vertical distribution of temperature, relative humidity and saturation deficit in Mixed forest.*

The observations were made with a whirling hygrometer shaded from direct sunlight. Relative humidities and saturation deficits are calculated assuming a barometric pressure of 760 mm.

(*a*) Measurements made on Baromalli tree.

	Breast height	Below canopy (*c.* 20 m.)	Canopy (*c.* 27 m.)	Above canopy (*c.* 33 m.)	Date and weather
Temperature (° C.)	24·7	—	26·1	25·4	Oct. 13
Relative humidity (%)	95·72	—	84·7	85·2	After slight shower
Saturation deficit (mm.)	0·99	—	3·85	3·56	
Temperature (° C.)	26·7	29·7	30·3	30·6	Oct. 17
Relative humidity (%)	89·5	66·6	63·1	59·7	Dry and sunny
Saturation deficit (mm.)	2·73	10·35	11·82	13·16	
Temperature (° C.)	27·4	29·5	29·6	29·5	Oct. 29
Relative humidity (%)	87·9	73·1	69·7	70·0	Just after slight
Saturation deficit (mm.)	3·43	8·25	9·31	9·08	shower
Temperature (° C.)	27·6	30·5	30·8	29·7	Nov. 6
Relative humidity (%)	87·4	60·2	60·5	59·6	Dry
Saturation deficit (mm.)	3·44	12·91	13·06	12·53	
Temperature (° C.)	27·6	29·6	30·3	30·3	Nov. 9
Relative humidity (%)	88·1	77·7	—	67·0	Bright sun with
Saturation deficit (mm.)	3·25	7·86	—	10·5	passing clouds: no rain

All these measurements were made between 1 and 2 p.m., except those on October 13th, which were made between 3.15 and 3.30 p.m.

(*b*) Measurements made on "Entomologists' Tree."

B.H.—breast height.

	8 a.m.		11 a.m.		5.30 p.m.			
	B.H.	26 m.	B.H.	26 m.	B.H.	26 m.		
Temperature (° C.)					26·1	28·9		Sept. 9
Relative humidity (%)					95·9	69·4		
Saturation deficit (mm.)					1·04	9·06		
	8 a.m.				6 p.m.			
	B.H.	26 m.			B.H.	26 m.		
Temperature (° C.)	22·9	23·9			26·1	26·7		Sept. 10
Relative humidity (%)	96·4	93·0			96·7	91·1		Fine, dry
Saturation deficit (mm.)	0·74	1·54			0·83	2·32		day
	8.30 a.m.		2 p.m.					
	B.H.	26 m.	B.H.	26 m.				
Temperature (° C.)	23·5	26·7	27·2	29·4				Sept. 11
Relative humidity (%)	98·2	83·8	85·8	54·4	—			Fine day
Saturation deficit (mm.)	0·38	4·14	3·81	13·9				
	8 a.m.		11 a.m.		5.30 p.m.			
	B.H.	26 m.	B.H.	26 m.	B.H.	26 m.		
Temperature (° C.)	22·2	23·3	26·1	27·8	23·9	23·9		Sept. 16
Relative humidity (%)	94·6	95·6	95·8	78·6	100	100		Showery
Saturation deficit (mm.)	1·08	0·94	1·04	5·94	0	0		
	7.30 a.m.							
	B.H.	26 m.						
Temperature (° C.)	22·9	24·4	—		—			Sept. 17
Relative humidity (%)	100	95·7	—		—			Dry and
Saturation deficit (mm.)	0	0·98	—		—			sunny
			11 a.m.					
			B.H.	26 m.				
Temperature (° C.)	—		26·8	30·1	—			Sept. 18
Relative humidity (%)	—		99·2	60·5	—			Dry day
Saturation deficit (mm.)	—		0·21	12·52	—			

Table VI. *Temperature, relative humidity and saturation deficit in the undergrowth of different types of forest.*

As it was not possible to make simultaneous observations of the temperature and relative humidity in different places, successive observations were made during journeys in which several forest types were traversed within short intervals of time. In most cases observations were made in the early morning (when the humidity throughout the forest was rising) and on the homeward journey (when it was either stationary or decreasing).

All observations were made at a height of 1–2 m. above the ground and a whirling hygrometer was used. Relative humidities and saturation deficits are calculated assuming a barometric pressure of 760 mm.

The arrows in the table indicate the order in which the different observations were made on each occasion.

No observations were made in Greenheart forest.

While little importance can be attached to the absolute values of the means of temperature, relative humidity and saturation deficit in the different types of forest, it may be concluded from the figures that in the day-time:

(1) The mean temperature is lowest in Mora and rises progressively through Morabukea and Mixed to a maximum in Wallaba.
(2) The mean relative humidity is highest in Mora and falls progressively through Morabukea and Mixed to a minimum in Wallaba.
(3) The mean saturation deficit is lowest in Mora and rises progressively through Morabukea and Mixed to a maximum in Wallaba.
(4) The temperature, relative humidity and saturation deficit fluctuate more widely in Wallaba than in any other type of forest. It seems likely that Greenheart would be found to be intermediate between Mixed and Wallaba in respect of all three factors.

			Forest type														
			Mora				Morabukea				Mixed				Wallaba		
Date	Times of first and last observations	Weather	Temp. (°C.)	Relative humidity (%)	Saturation deficit (mm.)		Temp. (°C.)	Relative humidity (%)	Saturation deficit (mm.)		Temp. (°C.)	Relative humidity (%)	Saturation deficit (mm.)		Temp. (°C.)	Relative humidity (%)	Saturation deficit (mm.)
Sept. 19	8–9 a.m.	No rain	23·3	100	0	↑	22·2	100	0	↑	—	—	—	↑	25·0	99·2	0·20
„ 28	9–10 a.m.	Weak sun	25·7	96·6	0·83	↑	26·0	94·1	1·46	↑	—	—	—	↑	26·9	91·2	2·33
Oct. 7	9–10 a.m.	—	25·6	93·3	1·63	↑	25·8	93·3	1·64	↑	—	—	—	↑	26·4	86·3	3·50
„ 7	2.45–3.15 p.m.	—	26·9	95·0	1·30	↓	27·5	91·2	2·39	↓	—	—	—		28·3	83·0	4·83
„ 8	9–9.30 a.m.	Sun with clouds	24·0	98·3	0·38	↑	24·7	99·1	0·20	↑	—	—	—		—	—	—
„ 11	9.35–9.56 a.m.	Light clouds	22·8	97·3	0·56	↑	23·1	97·3	0·56	↑	25·4	95·8	1·01		—	—	—
„ 12	8.47–9.6 a.m.	Weak sun	23·6	100	0	↑	24·7	100	0	↑	24·9	100	0	↑	26·1	95·1	1·24
„ 12	3.58–4.20 a.m.	Light cloud: about half-an-hour after a shower	25·4	97·5	0·61	↓	25·6	97·5	0·62	↓	25·6	94·2	1·42		—	—	—

Date	Time	Weather	Temp °C	RH %	Sat. def. mm	Temp °C	RH %	Sat. def. mm		Temp °C	RH %	Sat. def. mm		Temp °C	RH %	Sat. def. mm
Oct. 17	11.7–11.40 a.m.	Sun with clouds	26.4	96.7	0.84	26.5	92.7	1.85	↑	26.5	91.1	2.30		—	—	—
„ 17	8.15–8.45 a.m.	Weak sun	22.4	98.2	0.36	24.6	96.5	0.79	↓	24.9	95.7	1.00		—	—	—
„ 19	9.20–9.51 a.m.	Cloudy	26.4	100	0	24.7	94.9	1.18	↑	—	—	—	↑	25.6	96.6	0.82
„ 23	— to 10.7 a.m.*	Sun and passing clouds	25.7	88.5	2.83	25.8	87.4	3.12	↑	—	—	—	↑	26.7	86.4	3.54
„ 23	3.30–3.55 p.m.	Sunny	27.8	91.3	2.41	27.5	89.7	2.81	↓	24.6	96.5	0.79		29.2	66.9	9.97
„ 26	8.25–8.50 a.m.	—	23.1	97.3	0.56	24.0	99.3	0.19	↑	26.7	83.3	4.35		—	—	—
„ 26	3.55–4.20 p.m.	Sun with clouds	26.1	91.0	2.26	26.1	88.6	2.86	↓	—	—	—	↑	25.1	93.2	1.61
Nov. 2	8.50–10.20 a.m.	Sun with clouds	22.7	92.8	1.47	23.9	99.1	0.19	↑	—	—	—		28.8	85.5	4.26
„ 2	2.30–2.54 p.m.	Sun with clouds	24.6	89.9	2.33	27.8	90.6	2.62	↓	—	—	—	↑	26.1	91.8	2.05
„ 7	9.12–9.35 a.m.	Sun with passing clouds	23.6	96.7	0.71	25.0	94.1	1.40	↑	—	—	—		—	—	—
„ 7	2.40–3.5 p.m.	Sun with passing clouds	26.4	97.5	0.34	27.2	91.2	2.36	↓	—	—	—	↓	29.2	67.6	9.76
„ 9	8.54–9.29 a.m.	—	23.9	94.8	1.15	25.0	94.9	1.20	↑	25.3	90.8	2.20		—	—	—
„ 9	About 10.54 a.m.	—	26.1	95.9	1.04	26.4	85.6	3.69	↓	26.4	85.6	3.69		—	—	—
	Mean		24.9	95.7	1.04	25.4	94.1	1.48		25.6	92.6	1.86		27.0	86.9	3.68

	Mean difference in		
	Temperature °C	Relative humidity %	Saturation deficit mm
Between Mora and Morabukea			
Mean difference	+0.55	−1.6	+0.44
Standard deviation of the mean difference	0.21	0.46	0.18
Probability that the difference is significant (%)	99	>99	98
Morabukea and Mixed			
Mean difference	+0.3	−2.4	+0.59
Standard deviation of the mean difference	0.09	0.62	0.16
Probability that the difference is significant (%)	>99	>99	>99
Mixed and Wallaba			
Mean difference	+1.1	−4.3	+1.44
Standard deviation of the mean difference	0.5	3.3	1.0
Probability that the difference is significant (%)	97	81	85

* Time of first observation not noted.

it is attached. Twining climbers occasionally have a marked constricting effect on young trees, so that if they are unwound from the host a deep spiral groove is seen on its trunk.

Seedlings of canopy climbers are common in the undergrowth, but immature specimens reaching to heights between the canopy and the ground are hardly ever found, so presumably the intermediate stage is passed through very rapidly.

(4) *Distribution of epiphytes.*

Epiphytes are more abundant in the Guiana forest than in the lowland forests of Malaya, but considerably less so than in the mountain forests of the West Indian islands or in the temperate rain forests of New Zealand: the bulk and luxuriance of epiphytic vegetation is certainly less, though the number of species is probably as great or greater. The trunks of the trees never bear more than a few scattered epiphytes and even the upper boughs of large trees are only occasionally thickly covered with them. On the first two clear-felling plots (see p. 363), out of 193 trees over 5 m. high, only 30, and on the third out of 55 trees over 14 m. high, only 21, had any vascular epiphytes at all (neglecting small seedlings)[1]. However, the total bulk of vascular epiphytic vegetation over any area of ground is probably often equal to, and sometimes greater than, the bulk of its herbaceous undergrowth. The number of species of epiphytes of any area is certainly always much greater than the number of ground herbs. On the whole of our area at Moraballi Creek we collected about 114 species of vascular epiphytes (of which about 50 were orchids), but the actual number may very likely be twice as great. The number of ground herbs (not including those in recent second growth) was 123 (of these about 33 were confined to the creek bank) and the collection was certainly nearly exhaustive. All the epiphytes of our area belong to the group of "typical" epiphytes of Oliver (**15**): there are no "occasional" or "ephemeral" epiphytes, presumably owing to the poverty and specialised nature of the ground flora. The "hemi-epiphytes" have been included in the last section with the climbers.

The factors which determine and differentiate the habitats of epiphytes in a climatically uniform area such as ours are chiefly illumination, atmospheric humidity (which here depends mainly on degree of exposure to sun and wind) and character of bark (depending largely on the age and species of the tree). The large amount of humus accumulated is probably responsible for the abundance of epiphytes on most very large old trees, but the amount of humus is always very small compared with that found on trees in New Zealand (**15**). As noticed by Schimper (**16**, p. 91) epiphytes do not show any sort of regular stratification; they are too much affected by slight local variations

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[1] This was in Mixed forest. In the damper Mora type epiphytes are more abundant, in the drier Wallaba type they are scarcer.

in illumination, such as are produced by the difference between the density of the foliage of one species of tree and another.

There is undoubtedly some kind of succession of epiphytes with the age of the tree, but in the absence of exact knowledge as to the relative ages of individual trees, it cannot be easily made out, as the effect of age is hard to separate from that of the light, humidity and bark character factors. The pioneers are often Bromeliaceae (*Tillandsia* spp.), as already noted by Schimper (**16**, p. 93), also certain Araceae and ferns. Orchids on the whole belong to the later stages of succession.

An attempt is made in Table VII to show how the epiphytic flora varies with the size and species of the host tree. Each line refers to a single tree.

Table VII. *Epiphytes on trees on the clear-felling plots (Mixed forest).*

* = in flower or young fruit.

Species of tree			Height m.	Epiphytes
Eschweilera Sagotiana Miers			6	—
,,	,,		8	—
,,	,,		10	—
,,	,,		17	Fern at first fork (13 m.).
,,	,,		20	—
,,	,,		21	—
,,	,,	*	25	Two large *Anthurium Jenmanii* Engl., *Elaphoglossum glabellum* J.Sm., *Peperomia* sp. and young *Tillandsia* sp. on trunk just above first fork (19 m.).
,,	,,		28	—
,,	,,	*	28	—
,,	,,	*	29	Large *Anthurium* sp. and *Philodendron demerarae* Gleason at first fork (21 m.); large *Anthurium* sp. at second fork; *Elaphoglossum glabellum* J.Sm. and young *Tillandsia* sp. on branches.
,,	,,	*	31	Large *Peperomia* sp. and *Tillandsia* sp. at first fork (17 m.); young *Tillandsia* sp., *Marginaria tecta* (Klf.) and *Microsorium surinamense* (Jacq.) sparingly on branches.
,,	,,		32	*Havetiopsis flavida* (Bth.) (shrub) in crown.
,,	,,		36	*Gnetum paniculatum* Spruce (parasite [1]), abundant, and *Havetiopsis flavida* (Bth.) (shrub) in crown; large *Anthurium* sp. and *Microsorium surinamense* (Jacq.) on branches. Young *Marcgravia* sp. and *Peperomia obtusifolia* (L.) in a fork.
,,	,,	*	38	—
Licania laxiflora Fritsch	,,		5	—
,,	,,		6	—
,,	,,		7	—
,,	,,		7	—
,,	,,		9	—
,,	,,		9	—
,,	,,		10	—
,,	,,		11	Young epiphytic Aroid at 7 m.
,,	,,		14	—
,,	,,		18	—
,,	,,		21	—
,,	,,		26	—
,,	,,		29	—

[1] See footnote 1, p. 382.

Table VII (*contd.*).

Species of tree			Height m.	Epiphytes
Licania laxiflora Fritsch (*contd.*)			31	Large *Anthurium* sp. on trunk at 26 m.
,,	,,		33	Unknown Aroid at first fork (15 m.).
Eschweilera decolorans Sandwith			5	—
,,	,,		5	—
,,	,,		6	—
,,	,,		6	—
,,	,,		6	—
,,	,,		7	—
,,	,,		13	—
,,	,,		15	—
,,	,,		18	—
,,	,,	*	19	—
,,	,,	*	26	—
,,	,,		28	—
,,	,,	*	29	Young Aroid on branch.
,,	,,		31	—
,,	,,		35	*Phthirusa monetaria* Sandwith (Loranth) in crown.
Licania venosa Rusby			5	—
,,	,,		5	—
,,	,,		6	—
,,	,,		6	—
,,	,,		7	—
,,	,,		7	—
,,	,,		9	—
,,	,,		11	—
,,	,,		13	—
,,	,,		18	—
,,	,,		18	—
,,	,,		19	—
,,	,,		21	—
,,	,,		22	—
,,	,,		24	—
,,	,,	*	26	—
,,	,,		27	—
,,	,,	*	28	*Anthurium trinerve* Miq. (Aroid) and an orchid on trunk just above first fork (14 m.); *Elaphoglossum glabellum* J.Sm. (fern). *Maxillaria uncata* Lindl. and another orchid, also young *Tillandsia* sp. on branches.
,,	,,	*	28	Large orchid at first fork (19 m.); *Anthurium gracile* (Rudge) (Aroid) and *Tillandsia* sp. on trunk just above; *Anthurium trinerve* Miq. (Aroid) and orchid on branches. Seedling *Clusia* sp. on branch at 16 m.
,,	,,	*	31	*Hymenophyllum* sp. at first fork (18 m.); *Tillandsia bulbosa* Hook. and two other spp., *Codonanthe confusa* Sandwith, *Scaphyglottis violacea* Lindl., *Fractiunguis reflexa* Schltr., *Maxillaria uncata* Lindl. and one other orchid, *Microsorium surinamense* (Jacq.) and *Elaphoglossum glabellum* J.Sm. (ferns) on branches.
,,	,,	*	32	Large Aroids on trunk at 7 and 11 m.; small orchid and *Tillandsia bulbosa* Hook. on branches.

Four "climax" societies of epiphytes can be recognised:

(*a*) *Society of shade epiphytes.* On undergrowth and occasionally on young canopy trees, also on very old, thick bush-ropes. This society is best developed

in the undergrowth layer (up to *c.* 14 m.), but may reappear at the bases of the crowns of tall trees if the foliage is thick enough. Thus *Hymenophyllum polyanthos* (Sw.) and *H. ciliatum* (Sw.), two of the commonest filmy ferns of this society were occasionally found growing in thick carpets of moss at 20 m. from the ground. The dominant species are filmy ferns (*Trichomanes* and *Hymenophyllum* spp.). The other members of the society are various other ferns, e.g. *Hecistopteris pumila* (Spreng.), stray Bromeliaceae and a minute species of *Peperomia*, *P. emarginella* (Swartz). Orchids are absent, except one species, *Cheiradenia cuspidata* Lindl., which is always found clinging to the smooth trunks of large trees at a height of about 1–2 m. (only in well-lit forests).

(*b*) *Society of sun-epiphytes.* This grows in the centre of the crown and along the larger branches of canopy trees, especially of very large ones. It includes the vast majority of the orchids, aroids and bromeliads, also most of the epiphytes in other families. Most of the members are creeping or erect herbs but there are a few shrubs, e.g. *Havetiopsis flavida* (Bth.). The chief species are: Orchidaceae, *Maxillaria uncata* Lindl., *Fractiunguis reflexa* Schltr., *Trigonidium tenue* Lodd., *Polystachya geraensis* Rodr., *P. foliosa* Rchb. f., *Scaphyglottis violacea* Lindl. and innumerable others; Bromeliaceae, *Tillandsia* spp., *Aechmea* spp.; Araceae, *Anthurium Jenmanii* Engl., *A. gracile* (Rudge), *Philodendron demerarae* Gleason, etc.

Piperaceae, *Peperomia obtusifolia* (L.) and *P. ouabianae* C.DC.; Gesneriaceae, *Codonanthe calcarata* (Miq.) Hanst.; Lentibulariaceae, *Orchyllium* (*Utricularia*) *Schimperi* (Schenk) (only once seen: in carpets of hepaticae); Cactaceae, *Epiphyllum* sp.; Ferns, *Elaphoglossum glabellum* J.Sm., much the most abundant species, also *Marginaria tecta* (Klf.), *Eschatogramme Desvauxii* (Kl.), *Microsorium surinamense* (Jacq.), *Polypodium nanum* Fée, etc. Stray members of this society may occur on the trunks of trees below the first fork.

(*c*) *Society of extreme xerophilous epiphytes.* This lives on the most exposed twigs and branches of large canopy trees and throughout the crowns of outstanding trees (though these are often quite bare of epiphytes). It is exposed to wind and sun much more than the last society and is therefore liable to frequent short periods of extreme drought and has a smaller humus supply. The conditions of life are reflected in the structure of the members, many of which are succulent. This society includes a few orchids, certain narrow leaved species of *Tillandsia*, e.g. *T. bulbosa* Hook., *Aechmea* spp. *Codonanthe confusa* Sandwith (Gesneriaceae), *Rhipsalis Cassytha* Gaertn. (Cactaceae).

(*d*) *Society of epiphytic parasites* (*Loranthaceae*). These green parasites are abundant on the canopy trees, especially on those which are old and tall. Seven species were met with. A single tree may have as many as three species of parasites on it. Each species of parasite seems to have a great variety of hosts, but Greenheart (*Ocotea Rodioei* (Schomb.)) is a favourite. This society is

found mainly in the outer part of the crown of the host, so that it lives in an external environment much like that of the last society[1].

The forest type has a remarkable influence on the vertical distribution of these epiphytic societies. In Mora and Wallaba, the two "extreme" types, epiphytes are common near the ground. *Tillandsia* spp. may be found in flower within 3 m. of the ground and if, as often happens, the bough on which a large individual of *Tillandsia* sp. is growing breaks off and falls to the ground, it will continue to grow quite successfully. Plants are also sometimes found rooted in the ground, not attached to a branch: these have probably survived after the branch on which they grew has decayed away. There was no evidence that Tillandsias ever germinated on the ground. *Anthurium Jenmanii* Engler and other species occur on tree trunks to less than 3 m. from ground. Orchids are common at 2–4 m. from the ground and they continue to flourish on fallen branches. The epiphytic fern *Marginaria tecta* (Klf.) was once found at about 1 m. in Wallaba forest and at 1·5 m. in Mora. In the three central types of forest epiphytes (except the "shade society") are seldom visible from the ground. Tillandsias never occur below about 18 m. except for stray individuals, which are small and do not flower, on the taller undergrowth trees (lowest record for a mature plant 9 m.: only seedlings at still lower levels) and Tillandsias on fallen branches die quickly. *Anthurium Jenmanii* Engler was never seen below 17 m.: orchids never below 15 m. *Marginaria tecta* (Klf.) was once seen as low as 7·5 m., but it normally grew very much higher. Thus in the central types the altitudinal distribution of epiphytes is much higher than in the "extreme" types. In the latter the sun epiphyte society descends nearly to the ground and in Wallaba forest the shade society is wanting. In this type all the epiphytes of the taller canopy trees belong to the "extreme xerophilous" society. In the three "central" types the average heights of the epiphytic societies is highest in Morabukea forest.

Now these five types of forest differ both in illumination (owing to differences in the density of the canopy and in the amount of undergrowth) and in the humidity of the air in the lower levels. Either factor might control the average height at which the epiphytes grow. The illumination varies regularly from Mora to Wallaba, falling from a maximum in Mora to a minimum in Morabukea and rising again steadily through the other two central types to a second maximum in Wallaba[2]. The humidity of the air has a maximum in Mora and Morabukea and falls towards a minimum in Wallaba (see Table VIII).

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[1] *Gnetum nodiflorum* Brongn. and *G. paniculatum* Spruce are often found mixed with the Loranthaceae. So far as we can remember they grew in all cases as true epiphytes, *not* as lianes rooting in the ground (as stated in text-books and descriptions): they may have been partly parasitic like the Loranths they so closely resembled. Unfortunately we made no notes on the subject in the field.

[2] The actual values for illumination at breast height, expressed as fractions of full sunlight are: Mora, $\frac{1}{75}$, Morabukea, $\frac{1}{163}$, Mixed, $\frac{1}{150}$, Greenheart, $\frac{1}{123}$, Wallaba, $\frac{1}{10}$. For further details, see Part II.

It will be seen that the altitudinal distribution of the epiphytes varies in a manner exactly parallel with the variation in illumination, but shows no relation to the variation in atmospheric humidity (though the total abundance of epiphytic vegetation may be related to this factor). Light therefore seems to play the chief part in controlling the vertical distribution of epiphytes.

(5) *River bank forest.*

On the banks of the large rivers the canopy may be described as curving down to the water-level. The canopy trees send out flowering branches nearly from the base and the mantle of bush-ropes binds the forest margin into a solid wall of foliage[1]. Most of the epiphytes which in the interior of the forest are only found at great heights on the river banks are found occasionally within reach of the ground. Hence it is that these canopy epiphytes and lianes are better represented than might be expected in the collections of the early travellers who collected mainly on the banks of the great rivers and did little tree felling. Our intensive collecting in the tree-tops did not produce as many new species as might perhaps have been expected.

A feature of the river bank forest which Anderson (**17**, p. 4) noticed is that "...the forest trees are always found growing much more abundantly and closely together than on the lands immediately behind, and so close is the growth in places that two or three trees are often seen touching each other at their bases." This fact we also often observed, both on the Essequibo and the Cuyuni. Its chief cause is probably the better illumination of the river margins, compared with the forest interior.

IV. SUMMARY.

1. The district whose vegetation is described is only a few miles in extent and lies in the rain forest region of British Guiana in lat. 6° 11′ N.

2. The chief characteristics of the climate are high and even temperature (mean annual 25·9° C.) and constantly high humidity. Mean annual rainfall 270 cm. There are two dry seasons in the year, but no month has an average rainfall of less than 10·7 cm. In relation to these conditions the vegetation shows little periodicity, though there is some indication of two flowering seasons in the year.

3. Human interference has been one of the most important biotic factors. It has chiefly taken the form of shifting cultivation and timber (Greenheart) exploitation. The latter is much the more important at the present time. Its effects can be mostly allowed for in ecological work.

4. The structure of the forest is described in some detail. The trees form only two distinct strata, an irregular canopy of about 24 m. average height and under-growth trees up to about 14 m. high. Above the former many trees of up to

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[1] The dense curtains of *Lygodium micans* Sturm are particularly characteristic of the banks of the lower Cuyuni.

42 m. stand out incompletely, while here and there are exceptionally tall trees which have their whole crown clear of their neighbours. The stratification of the trees was shown by felling and measuring all the trees on sample plots. Two strata of herbs and shrubs are recognised and the former are grouped into a number of synusiae. The stratification of the climbers and the distribution of the epiphytes is mainly a response to the internal climate of the forest determined by the vegetation itself. This internal climate differs from the general climate of the region in its even more extreme uniformity, which increases from the canopy downwards.

5. The height at which the epiphytes grow is shown to depend mainly on light intensity and to be hardly at all related to differences in the humidity of the air.

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A COMPARATIVE STUDY OF THE ALGA FLORA OF TWO SALT MARSHES[1]. PART III

(Concluded)

By NELLIE CARTER.

(With three Figures in the Text.)

CONTENTS.

X. THE ECOLOGICAL COMMUNITIES OF ALGAE.

THE phanerogams on a salt marsh are readily separated into communities owing to the clear way in which they occur in vertical zones in relation to level. The zonation of the algae is not nearly so obvious. Many of the forms, especially the larger and more conspicuous green algae of the salt marsh, such as *Enteromorpha, Rhizoclonium* and *Vaucheria*, are to be found at all levels, provided that space is available and the illumination is sufficient. It would appear that light and space relations, rather than factors more intimately related to level, restrict the development of these algae in the *Glyceria* zone at Canvey. Similarly, the most striking blue-green alga of the salt marsh, *Microcoleus chthonoplastes*, shows no zonation in relation to level and occurs in all parts of the marsh.

There are many other algae commonly found on the salt marsh, however, which show zonation of distribution to some extent, but there are not so many zones of algae as there are of phanerogams, indicating a much greater plas-

ticity on the part of the algae as compared with the higher plants. The algae are not nearly so restricted in their requirements, and consequently spread over a much wider range. As a rule it is not possible to divide the algae into more than two groups, one preferring the lower zones, and another set preferring the upper zones (Figs. 1, 2), but owing to the plasticity referred to above, there is considerable overlapping, e.g. on the escarpment between the *Aster-Salicornia* and marginal zones (Fig. 1). The "lower zones" would constitute at Canvey the *Aster-Salicornia* zone and all areas of lower level; at Ynyslas, the *Marginal mud* and Salicornietum only. The upper zones include at Canvey the *Glyceria* zone and all parts of the marsh extending down to, but not including, the *Aster-Salicornia* zone; at Ynyslas everything above the Glycerietum is included.

The Chlorophyceae probably provide the greatest bulk of the salt-marsh algae, and at the same time they are the most puzzling. The Cyanophyceae also play a very large part, and some of them fall into well-defined communities of more or less fixed specific constitution, in which other algae, either Chlorophyceae or diatoms, are rare or wanting. Others commonly occur in association with Chlorophyceae. It is a fairly well established fact that Cyanophyceae as a rule reach their highest development in the late summer months. Studies on the periodicity of algae have repeatedly proved this fact (see Fritsch (9), West (20), Hodgetts (13)). Some of the communities of Cyanophyceae observed on the salt marsh can only be found at certain times of the year. Whilst the Chlorophyceae are not, in general, differentiated into definite communities associated with level, the Cyanophyceae communities are often restricted to certain levels of the marsh.

The diatoms, as will be seen from a consultation of Carter (6, p. 171), conform in general to the usual plan, that certain species prefer the upper levels of the marsh, and others the lower. An attempt was also made there to subdivide the diatoms further according to level, but whether this is desirable further study must prove. Diatoms sometimes dominate the habitat, as in the case of the marginal zones, but more often they occur scattered amongst other algae in such a way that it is impossible to associate any particular diatom with any particular alga, the same diatoms usually occurring amongst *Vaucheria* as amongst Cyanophyceae at the same level, or even on bare ground in the vicinity which bears no larger algae.

The following communities are to be regarded as instances of species definitely associating in the same habitat, but exactly what is their ecological status must be left for the future to decide. The first community has a wide range and is represented in some degree all over the salt marsh, though not all of the component species are invariably present. The next five communities are more particularly characteristic of the lower zones of the marsh, and the last six of the higher zones.

I. *General Chlorophyceae community.*

Vaucheria spp. L.D.[1]
Enteromorpha prolifera L.D. (see Carter (**6**, p. 134))
E. percursa L.D.
Microcoleus chthonoplastes L.C.
Lyngbya aestuarii L.C.
Rivularia spp. L. (Y.)
Gloeothece palea L. (Y.)
Microcolous tenerrima L.
Rhizoclonium hieroglyphicum L.D.

Hydrocoleum lyngbyaceum L.C. (Y.)
Lyngbya lutea L.C. (Y.)
Nostoc commune L.C. (Y.)
Spirulina subsalsa O.
Oscillatoria corallinae O.
Phormidium angustissimum R.
Ph. foveolarum R.
Plectonema phormioides R. (Y.)
Phaeococcus adnatus R.

Cotton (**8**, pp. 62–5, 78–80) recognises in the sand and sandy mud habitats of Clare Island and the neighbouring regions, amongst others, three communities dominated by *Rhizoclonium riparium*, *Microcoleus chthonoplastes* and *Vaucheria Thuretii* respectively, whilst in the more muddy regions rich in humus and referred to as salt marsh, a second *Rhizoclonium riparium* community is recognised, differing from the first in its greater variety of associated species. It is stated that on sand *Rhizoclonium* is sometimes accompanied by *Microcoleus chthonoplastes*, but the blue-green species (i.e. *Lyngbya aestuarii*, *L. majuscula* and *L. confervoides*) so common in the corresponding association on the salt marsh, are absent (p. 63). In the *Vaucheria* community Cotton sometimes also found *Rhizoclonium*, *Chaetomorpha* and *Cladophora fracta*; in the *Microcoleus chthonoplastes* community, *Lyngbya aestuarii*, *L. lutea*, *Microcoleus chthonoplastes*, *Vaucheria Thuretii*, *Rhizoclonium riparium* and *Enteromorpha torta*.

A comparison of the above lists will show that practically all the species mentioned by Cotton in the four communities referred to also occur in the community we are here considering. The writer does not feel, however, from her own observations, that the algae listed together as community No. I can be separated into smaller communities, at any rate in the two marshes under consideration. It may be, of course, that at Canvey and at Ynyslas there are several smaller communities competing with each other, but at Ynyslas, in particular, the algae were so frequently in association with one another that separate communities of smaller size seemed out of the question. The algae of community No. I occupy the interstices between the phanerogams in all zones above the Glycerietum at Ynyslas (Fig. 2), being feebly represented in that zone probably because of the shifting sand. It also extends on the Canvey marsh through all the zones from the *Aster-Salicornia* zone up (Fig. 1). Represented by *Vaucheria* in practically pure stands, it may also descend at Canvey into the upper stretches of marginal mud destitute of phanerogams.

The Ynyslas marsh seemed on the whole to provide algal vegetation corresponding best with that described by Cotton for Clare Island, with the exceptions just mentioned. In view of its similar coarse sandy substratum this is to be expected. *Rhizoclonium* is by far the commonest dominant at all times of the year. From September to March *Enteromorpha percursa* seemed

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[1] L.D. locally dominant; L.C. locally common; L. local; O. occasional; R. rare; (Y.) Ynyslas only.

sometimes to be dominant locally, especially at the level of the Armerietum and below, and at the same levels *Enteromorpha* sp. was frequently present. *Vaucheria* seemed to dominate locally in slightly moister spots which are not, however, often disturbed by tides, such as around the margins of pans which remain full. The Cyanophyceae, of which *Microcoleus chthonoplastes* is the most general, accompanied by *L. aestuarii* and often *L. lutea*, sometimes dominate quite small areas an inch or so in diameter at any level above and including the Armerietum, more particularly in the summer and autumn (cf. Fig. 2, I, *B*). More often however the blue-greens are to be found as a tough felt forming a ground flora underlying *Vaucheria* or *Rhizoclonium*. They are often associated with *Vaucheria*, especially in the late summer months if the weather has been dry. *Rhizoclonium* and *Enteromorpha* seem unable to withstand drought, so that *Vaucheria* and the Cyanophyceae then become increasingly important. Under ordinary conditions Cyanophyceae are more abundant in the higher zones, from the Lower Festucetum up.

Thus it will be seen that the algal vegetation is likely to be patchy, the dominants varying at quite short range, usually within a few inches. It is indicated that weather, as for example a period of drought, may influence the dominating forms. Possibly there is continual competition between all the important algae, whose requirements are nearly similar: thus a slight change in the external conditions might so disturb the balance as to give an advantage to one particular alga.

At Canvey, the community is very different, as it consists as a rule only of *Enteromorpha prolifera* and *Vaucheria* spp. *Rhizoclonium* is never abundant as a soil form, and *Enteromorpha percursa* seems to have no real place here. *Vaucheria* persists all the year round, but *Enteromorpha* is almost wanting from September to March. There are almost no other algae associated either with the *Vaucheria* or the *Enteromorpha*. The algal vegetation forms a coarser patchwork here than at Ynyslas, for instead of occupying small areas, one or other of these algae may dominate areas several feet in diameter. It would appear that *Vaucheria* prefers a substratum where changes in topography are causing the accretion of silt, whilst *Enteromorpha* prefers more stable areas. *Microcoleus chthonoplastes* is the only important associate of these two Chlorophyceae except in the late summer and autumn, when other communities of Cyanophyceae begin to invade their area, e.g. communities Nos. III, VI and VIII. Many of the blue-green components of community No. I represented at Ynyslas do not occur at Canvey, e.g. *Hydrocoleum lyngbyaceum*, *Gloeothece palea*, *Rivularia* spp. and *Nostoc commune*. *Phaeococcus adnatus* and *Microcoleus tenerrima*, although present at Canvey, are very restricted in their distribution.

After a study of this algal community one comes to the conclusion that it would be difficult to fit it into the existing scheme of salt-marsh vegetation as an independent community. In nearly all the area occupied by this group

of algae (except when it extends out on the open mud) the phanerogams are the conspicuous plants, and consequently it would not be correct to consider it as a separate algal "association." The algae are merely adjuncts to the phanerogam vegetation of each zone. Thus we can briefly state the facts as follows:

Ynyslas. The Juncetum, Upper and Lower Festucetum, Armerietum and Glycerietum support, in addition to their phanerogam vegetation, Algal Community No. 1, with the proviso that the Cyanophyceae constituents of the Armerietum and Glycerietum are likely to be less abundant than in the higher zones.

Canvey. The *Aster-Salicornia, Aster-Glyceria, Obione* and *Glyceria* zones support, in addition to their phanerogam vegetation, Algal Community No. 1, with the proviso that their Cyanophyceae constituents are not usually abundant.

Cotton (**8**) does not give the phanerogam flora of his area, and Lloyd Praeger (**15**) in his account of the phanerogams and ferns does not give very much information about the salt marshes of the Clare Island region. Thus it is not possible to deduce from the Reports of the Clare Island Survey what relation the algal associations described by Cotton bear to the flowering plants. It is possible that in Clare Island the algae themselves and not the phanerogams are the real dominants.

II. *Marginal community of diatoms.*

DIATOMS D.[1]

Euglena limosa L.	Holopedia sabulicola R.
Microcoleus acutirostris O.	Merismopedia revoluta R.
M. chthonoplastes O.	M. convoluta R.
Pseudanabaena brevis (sporadic)	

The chief diatoms are:

Pleurosigma angulatum includ. var. quadratum V.C. or D. (W.)	Navicula gregaria C. (S.)
Surirella gemma V.C. or D. (W.)	N. cincta var heufleri C. (S.)
Gyrosigma Wansbeckii V.C. or D.	Nitzschia navicularis O.
G. balticum V.C.	Navicula (Diploneis) elliptica O.
Nitzschia rigida V.C. or D. (W.)	Rhaphioneis amphiceros O.
Navicula pygmaea V.C. or D. (W.)	Navicula litoralis O.
N. digito-radiata var. cyprinus V.C. or D. (W.)	Amphora proteus O.
Scoliopleura tumida V.C. or D. (S.)	Stauroneis Gregorii O. (S.)
Nitzschia acuminata V.C.	Navicula spuria O.
Navicula subinflata V.C. (S.)	Nitzschia bilobata R.
Nitzschia apiculata V.C.	Scoliopleura latestriata R. (S.)
Gyrosigma diaphanum V.C. (W.)	Gyrosigma Fasciola R. (W.)
Amphora lineolata C. or D. (S.)	Navicula humerosa R.
Navicula ammophila var. flanatica C.	N. (Diploneis) didyma R.
N. hemiptera L.C. (S.)	Nitzschia epithemioides R. (S.)
Gyrosigma Spenceri V.C.L.	Nitzschia punctata R.
G. litorale C.	Melosira (Paralia) sulcata R.
Surirella ovalis var. ovata C.	Biddulphia Smithii R.
Gyrosigma attenuatum var. scalprum C. (S.)	B. aurita R.
	Actinoptychus undulatus R.[2]

[1] V.C. very common; L. local; D. dominant; O. occasional; R. rare; C. common. (S.) denotes species with a summer maximum. (W.) denotes species with a winter maximum. Both (S.) and (W.) may be present in slight quantity all the year round, but are usually rare except in their respective seasons. Dominance by a particular diatom is not constant, but the species noted as V.C. will often be exceedingly abundant.

[2] Figs. 8, 13, 21, 22, 23 and 24 in Part II (see **Carter, 6**) illustrate many of these algae.

Many of the diatoms show a summer or winter maximum (see also Carter (**5**), p. 354). This is indicated in the list on p. 389, and also in Fig. 3, *C* and *D*.

This community is usually apparent as a brownish film on the marginal mud of channels at Canvey, both large and small, and it is here that it reaches its highest development (Fig. 1, II). At Ynyslas it is only represented as a rule by a few individuals which can be obtained from the apparently bare

DISTRIBUTION OF COMMUNITIES, CANVEY
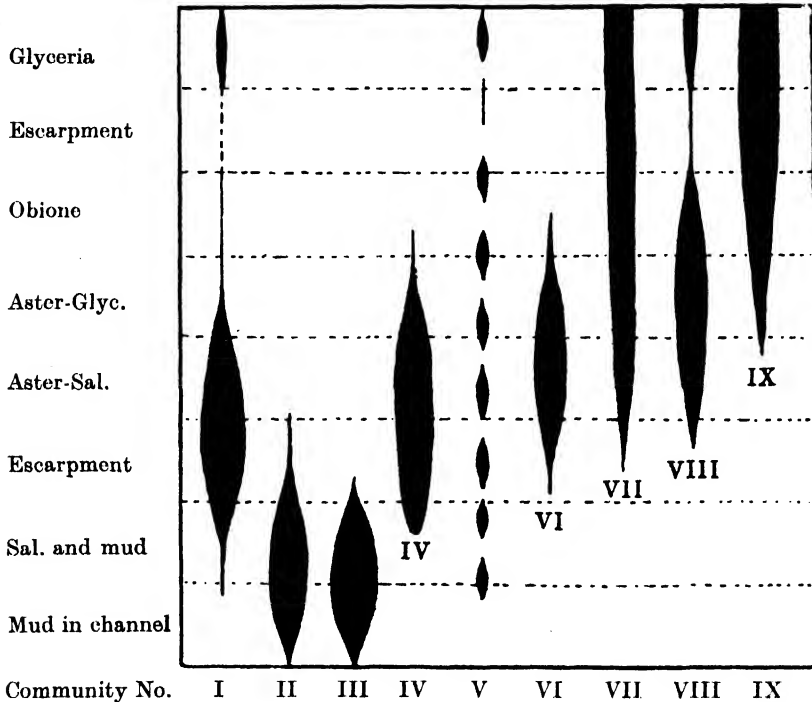
FIG. 1. Showing the range of the algal communities in the zones of the marsh at Canvey. I, general Chlorophyceae community. II, marginal community of diatoms. III, marginal Cyanophyceae community. IV, *Ulothrix flacca* community. V, *Enteromorpha minima-Rhizoclonium* community. VI, *Anabaena torulosa* community. VII, filamentous diatom community. VIII, autumn Cyanophyceae community. IX, *Phormidium autumnale* community.

sand at the margins of the marsh, although the smaller channels are rather more productive. If *Euglena* is present, the fact will be revealed in the local bright green patches of colour in the surface film. The presence of *Pseudanabaena* causes a grey-blue coloration. The other Cyanophyceae are not usually present in sufficient quantity to be evident in the field, though they may be visible after a sample has been exposed to light for some time. As an exception, *Microcoleus chthonoplastes* may sometimes become so abundant as to form a tough sheet on the surface of the mud. This has been observed at Ynyslas in the autumn.

This marginal community has not previously been described and it ranks as an independent unit of vegetation, since it is not subsidiary to flowering plants. *Salicornia* is the only phanerogam occurring in this region, and since the plants are distant from each other, the cryptogams are usually relatively more important and give the mud its characteristic appearance. At Canvey there is a tendency for the community to extend into the *Aster-Salicornia* zone.

In the late summer months the upper parts of the channels at Canvey are occupied by a conspicuous growth of Cyanophyceae constituting community No. III, but the diatoms still remain and many of the same species can be recognised as before the invasion.

The flora of pans with standing water often includes diatoms as the most important forms, and to some extent the marginal diatom community is again repeated here. The origin of this pan flora, however, seems to be various. One example studied in January in which there was a copious development of brownish diatomaceous flocculent growth on the surface of the bottom mud, proved to consist largely of *Gyrosigma Spenceri, Nitzschia navicularis, Navicula gregaria, N. interrupta, N. (Diploneis) didyma,* etc., species for the most part which occur all over the marsh, or are characteristic of the higher zones. *Pleurosigma angulatum* and *Surirella gemma,* species characteristic of the marginal mud at that time of the year, were notably absent. On the other hand a sample of plankton taken from a similar pan in June showed a copious diatom flora in which *Navicula (Diploneis) didyma, N. gregaria, Amphora Proteus, Scoliopleura tumida, Navicula pygmaea, Pleurosigma angulatum, Navicula digito-radiata* var. *cyprinus, Nitzschia rigida* and *Amphora lineolata* figured. This list includes forms which are distinctly marginal ones, such as *Scoliopleura tumida* and *Pleurosigma angulatum.* These observations show that both marginal diatoms and at any rate some of those characteristic of the higher zones can persist in the standing water of a pan.

At Ynyslas community No. II is not developed to any great extent at the margins and is only represented by a few individuals of *Navicula cincta* var. *heufleri, Nitzschia rigida* or *Scoliopleura tumida.* Only very rarely is a visible brown stratum present, though at times the small green patches of *Euglena* or the dark sheets of *Microcoleus chthonoplastes* can be discerned. The smaller and less disturbed muddy channels draining the marsh, however, often develop the diatom community in a way comparable to the channels at Canvey. A sample taken from such a channel in July showed a flora of *Nitzschia rigida, Navicula digito-radiata* var. *cyprinus, N. cincta* var. *heufleri, Gyrosigma diaphanum, Nitzschia punctata* var. *coarctata,* and *Scoliopleura tumida.* All are marginal forms with the exception of *Navicula cincta* var. *heufleri* which is universal on the marsh. In a similar channel, but amongst *Rhizoclonium* near the upper margin of the channel, the diatom flora was similar, but included in addition a number of diatoms which frequent the upper zones, such as *Navicula (Diploneis) Smithii, N. (D.) litoralis,* as well as other species which

are ubiquitous for the marsh, e.g. *Navicula gregaria, N. subinflata* var. *elliptica, N. (Diploneis) didyma* and *Nitzschia navicularis.* Probably these additional species spread with the *Rhizoclonium* from the adjoining turf. Similarly a sample from the bottom flora of a pan at Ynyslas in July yielded forms which are partly marginal, such as *Nitzschia rigida, Gyrosigma diaphanum, Nitzschia punctata, N. acuminata, Scoliopleura tumida, Gyrosigma attenuatum* var. *scalprum* and *Amphora Proteus,* and partly species of unrestricted distribution or more characteristic of the higher zones, e.g. *Navicula gregaria, N. cincta* var. *heufleri, N. (Diploneis) didyma, N. (D.) litoralis, N. subinflata.*

The pans and smaller channels therefore seem to provide an intermediate habitat in which two types of diatoms, either marginal, or characteristic of the higher zones, may find shelter for a time. At times of tidal submergence, however, the vegetation is disturbed, so that no stable habitation is possible and it is impossible to say whether one or both types could survive the conditions indefinitely.

III. *Marginal Cyanophyceae community*[1].

Oscillatoria sancta Co-D.	S. subtilissima C.
O. corallinae Co-D.	Microcoleus chthonoplastes O.
Phormidium angustissimum C.	Oscillatoria formosa O.
P. tenue C.	O. lactevirens R.
Spirulina major C.	Phormidium foveolarum R.[2]
S. subsalsa C.	

In its typical form this community occurs from about July–October (Fig. 3, III) as a dark, almost black stratum, about 12–18 in. broad, lining the upper margins of channels at Canvey within a few inches of the upper vegetated margin (Fig. 1, III). It has not been observed at Ynyslas. As a rule the first two species are present in the greatest quantity, usually with one or more species of *Phormidium* or *Spirulina* admixed. Sometimes a more or less distinct film of Cyanophyceae may be visible on the marginal mud even as late as April, but the composition of the film is not typical of this community and is often restricted to a local growth of one or other of the various constituents. Thus in April, 1926, *Spirulina subsalsa* occurred in a pure stratum, and *Oscillatoria corallinae* is likely to be found at all times of the year, but the blue black film composed of the above mixture of forms is only typically produced in the late summer and autumn.

IV. Ulothrix flacca *community*[3].

Ulothrix flacca D.	Rhizoclonium hieroglyphicum subsp. riparium R.
U. subflaccida R.	Enteromorpha minima R.[2]

This is a strictly vernal community which makes its appearance in early January and begins to disappear in March or April (Fig. 3, IV). Often it consists of a pure growth of *Ulothrix flacca,* the other species being entirely

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[1] Many of these algae are figured in Part II (**Carter (6)**, Fig. 10).
[2] For abbreviations see footnote p. 389.   [3] Cf. Part II (**Carter (6)**, Fig. 1).

absent. The community appears in the upper margins of channels in the *Aster-Salicornia* and *Aster-Glyceria* zones. Beginning as a silky weft of threads in a few sheltered low-lying parts of the marsh, it spreads until all the lower zones of the marsh are covered by a delicate green carpet (Fig. 1, IV). In its development the alga envelops all pre-existing vegetation or débris. If there has been, at an earlier stage, a growth of *Vaucheria* or *Pylaiella*, this is all covered by the delicate cobwebby stratum; the remains of *Aster* and *Salicornia* plants, and the leaves of *Glyceria* which have been washed prostrate by tidal submergence are all festooned by this alga. In March or April, according to the time of neap tides, the weft becomes desiccated, fails to recover and is replaced by a vigorous growth of *Enteromorpha*.

V. Enteromorpha minima-Rhizoclonium *community*[1].

> Enteromorpha minima D.[2]
> Rhizoclonium hieroglyphicum subsp. riparium V.C.

This is essentially an epiphytic community which has only been observed at Canvey. The algae use as a substratum any plant which has a suitable rough exterior to provide anchorage, and in the course of the year various hosts serve. *Enteromorpha minima* occurs chiefly as sporelings about November to January. At this time of the year the remains of withered *Salicornia* plants and the basal parts of stout *Aster* stems are covered with a green blanket composed largely of this alga. Older *Enteromorpha* plants associated with *Rhizoclonium* retain the same habitat until about May, when the phanerogams begin to show their new growth, and the previous year's remains have at length become disintegrated. Masses of *Enteromorpha minima*, still attached to phanerogam débris, may sometimes be washed up by the tide. The perennial woody stems of *Obione* form a suitable habitat for this community all the year round, but the *Aster* and *Salicornia* remains provide the most important substratum in the particular season when they are available.

VI. Anabaena torulosa *community*[3].

> Anabaena torulosa D.[2]
> Nodularia Harveyana C.

This community is much more common at Canvey than at Ynyslas, but it was observed on one occasion at Ynyslas, overlying *Sphacelaria* lining the upper margins of some of the channels draining the salt marsh.

When the community is fairly pure and there is a large proportion of *Anabaena* present, it forms circular glistening patches varying from one to several centimetres in diameter, spreading as a thin, smooth film over bare soil, *Vaucheria* or any other alga which happens to have been previously in possession of the substratum. Frequently it mingles with community No. III, in which case the limitation of the colonies may not be as sharp. The duration

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[1] Cf. Part II (**Carter (6)**, Fig. 6, p. 146).   [2] For abbreviations see footnote p. 389.
[3] Cf. Part II (**Carter (6)**, Fig. 14).

of this community is very short, for it is rarely seen except in July and August (Fig. 3, VI). Its regular appearance, always in July, is most striking. In level it extends from the bare mud just beneath the *Aster-Salicornia* zone to the *Obione* and *Aster-Glyceria* zones (Fig. 1, VI). Johnson and York (**14**) describe the occurrence of the colonies of *Anabaena torulosa* in Cold Stream Harbour at a level of 4–6 ft. above mean low-tide mark.

DISTRIBUTION OF COMMUNITIES, YNYSLAS.
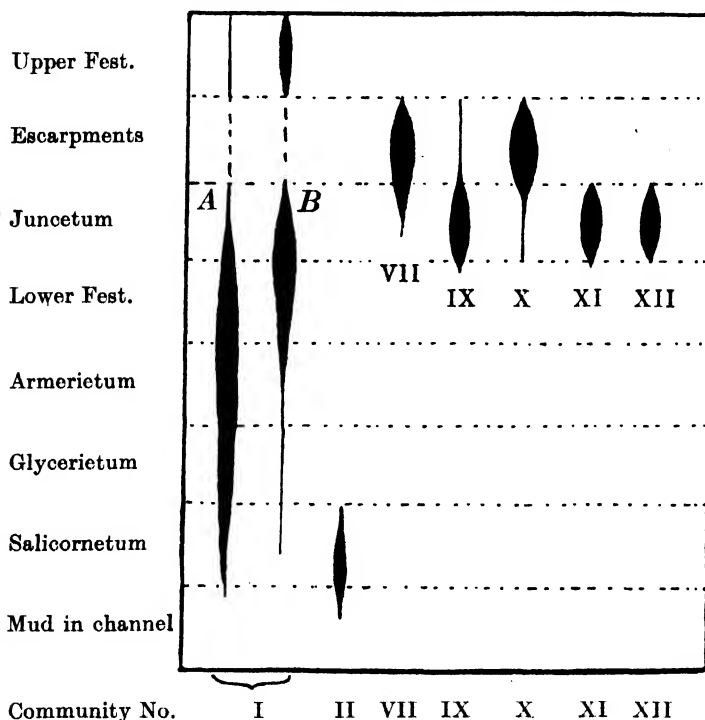
FIG. 2. Showing the range of the algal communities in the zones of the marsh at Ynyslas. I, general Chlorophyceae: *A*, Chlorophyceae components; *B*, Cyanophyceae components, which have, on the whole, a higher distribution on the marsh than *A*. II, marginal community of diatoms. VII, filamentous diatom community. IX, *Phormidium autumnale* community. X, *Rivularia-Phaeococcus* community. XI, *Pelvetia canaliculata* ecad *muscoides* community. XII, *Catenella opuntia-Bostrychia scorpioides* community.

VII. *Filamentous diatom community*[1].

Navicula (Schizonema) Grevillii L.D.[2]
Navicula (Schizonema) ramossissimum L.D.
Gyrosigma scalproides var. eximium L.D.
Diatoms of groups I, IV or V (see Part II, Carter (**6**), p. 171) subsidiary.

This community is seen best at Canvey, although even there its distribution is exceedingly limited. Wherever the soil is covered with an almost imperceptible brown film, as frequently happens in the *Aster-Salicornia, Obione* and *Glyceria* zones, the presence of this community is to be suspected (Fig. 1,

[1] Cf. Part II (**Carter (6)**, Fig. 18).   [2] For abbreviations see footnote p. 389.

VII). The community is not a seasonal one and is represented at most times of the year (Fig. 3, VII), although it is much more conspicuous in the winter months, since larger algae are rarer then and there is much more bare soil on which it can spread. Besides thus playing a part at times in the more densely vegetated parts of the marsh, this community is often of considerable importance as a pioneer community, as it is the first vegetation to establish itself on the surface of any soil which is out of reach of most ordinary tides. Thus, where channels have been cut deeply into the higher zones by strong tides, the margins often being undercut and with an overhanging sod held together mainly by the roots of phanerogams, this community of filamentous diatoms will probably be developed on the bare mud just beneath the phanerogams, where submergence is not frequent. Again, in the course of time, the contour of the larger channels continually changes in such a way as to produce hummocks of slightly higher level than the surrounding mud (cf. Part I, Carter (5), p. 366, and Part II, Carter (6), p. 183). The first vegetation to establish itself on the developing hummock is this filamentous diatom community. It is frequently invaded by filaments of Cyanophyceae or Chlorophyceae which represent later stages in the colonisation. At higher levels on the marsh, also, e.g. in the *Aster-Salicornia* or *Obione* zones, the community can also be recognised interspersed amongst *Anabaena, Phormidium* or other algae, which seem to come and go in their appropriate season without exterminating the diatoms. The community seems unable to tolerate soft mud or frequent tidal submergence and is therefore not developed so extensively on the mud of the channels as community No. II, preferring a firmer substratum which is not so frequently inundated. *Navicula (Schizonema) Grevillii* is the usual dominant, but *Gyrosigma scalproides* is nearly always present. *Navicula (Schizonema) ramossissimum* was only once observed to be dominant (June, 1929). The associated forms are such diatoms as *Navicula gregaria, N. cincta* var. *heufleri, N. ammophila* var. *flanatica, N. (Diploneis) litoralis* and *Gyrosigma Spenceri*, which as one can see at a glance, are chiefly diatoms characteristic of all zones or of the top zones only (cf. Part II, Carter (6), p. 171).

At Ynyslas, owing to the more closed nature of the vegetation this community is very rare, being represented only to a slight extent on vertical escarpments which have recently been eroded (Fig. 2, VII). Here it may frequently be found on firm soil which seems to be quite bare. *Navicula (Schizonema) Grevillii* is often the only representative and community No. X is usually present in greater abundance.

VIII. *Autumn Cyanophyceae community*[1].

Oscillatoria Bonnemaisonii Co-D.[2]   Microcoleus chthonoplastes Co-D.
O. nigro-viridis Co-D.   Lyngbya confervoides O.
O. brevis Co-D.

This community is essentially characteristic of the *Aster-Salicornia* and

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[1] Cf. Part II (Carter (6), Fig. 9).   [2] For abbreviations see footnote p. 389.

Obione zones at Canvey, rarely extending into the *Glyceria* zone (Fig. 1, VIII). Usually two or more of the first-mentioned species seem to be the dominant species, but there are usually at least three or four different Cyanophyceae and a number of diatoms present, representatives of groups I, II or III (cf. Part II, Carter (**6**), p. 171). The community is a seasonal one and lasts from about July to November (Fig. 3, VIII).

IX. Phormidium autumnale *community*.

Phormidium autumnale very frequently forms continuous sheets of considerable extent in the *Aster-Glyceria*, *Obione* and *Glyceria* zones at Canvey (Fig. 1, IX). It tends at times to mingle with community No. VIII, but so often does it occur alone that it seems to be an independent community. Further it seems to favour higher levels than the autumn community of Cyanophyceae, since it rarely descends as low as the *Aster-Salicornia* zone. The alga often occurs in pure sheets, in which there are no associates except a few diatoms. It is more important in late summer and autumn, becoming abundant in July and remaining so until about November (Fig. 3, IX). At Ynyslas the alga is often found in sheets covering the soil between clumps of *Juncus* in the Juncetum zone (Fig. 2, IX).

X. Rivularia-Phaeococcus *community*.

Rivularia atra D.[1]	Endoderma perforans C.
Phormidium molle C.	Phormidium autumnale O.
Phaeococcus adnatus C.	Navicula (Schizonema) Grevillii O.

This community is characteristic of vertical escarpments at Ynyslas (Fig. 2, X), and to a less extent at Canvey (cf. Part I, p. 365). It persists all the year round (cf. also Parts I and II, Carter (**5**), p. 364; (**6**), p. 169). Cotton (**8**, p. 82) has described the vegetation of vertical banks in salt marshes near Clare Island, which is similar to that of Ynyslas in including species of *Rivularia* and *Phaeococcus adnatus*. Cotton also includes in the community *Rhizoclonium riparium*, *Vaucheria coronata* and *Calothrix fasciculata*. There is a notable absence in the marsh at Ynyslas of both the latter species in the escarpment flora as far as present observations go. *Vaucheria sphaerospora* was observed at the margins of the marsh on one occasion; it was not, however, growing on a firm escarpment, but on soft low-lying mud. Cotton found that in the localities examined by him there was definite vertical zonation to be recognised in the alga. Thus *Rivularia Biassolettiana* occupied the top zone of 1 in., next came *Phaeococcus adnatus* occupying 2–6 in., followed by *Rivularia nitida*, 1 ft., with *Vaucheria* and *Calothrix*, 1–2 ft. and *Rhizoclonium* with *Fucus spiralis*, 1–2 ft. at the base of the escarpment. Thus according to Cotton *Rivularia* and *Phaeococcus* occupy up to 1 ft. 7 in. of the vertical height of the escarpments. At Ynyslas also, similar algae occupy equivalent areas of the

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[1] For abbreviations see footnote p. 389.

escarpments, but there was no obvious separation of the *Rivularia* and *Phaeococcus* into zones at Ynyslas, the area being generally strewn with *Rivularia* colonies, and the presence of the *Phaeococcus* on the soil between them was not suspected until discovered by microscopic examination.

The community is simplified considerably when it is represented on the somewhat rare escarpments which occur further back in the marsh at Canvey (see Part I, Carter (**5**), p. 365).

The writer has not included *Rhizoclonium riparium* and *Pylaiella litoralis* in this community because they do not seem to have any intimate relation with the above forms ecologically. The former seems to be an invader from the adjacent turf zones and is merely an accidental inhabitant of the escarpments, whilst *Pylaiella* is only a vernal form and is likewise only an incidental inhabitant (see also Carter (**5**), p. 364). Neither occupies the substratum in the same way as *Rivularia* and *Phaeococcus*, etc., both being much more superficial in their habit (cf. Carter (**5**), p. 365).

XI. Pelvetia canaliculata *ecad* muscoides *community*.

This community persists all the year round (Fig. 3, XI). Cotton (**8**) has described an association of *Fucus vesiculosus* var. *muscoides* which cover considerable areas on peaty shores and on the salt marshes of the Clare Island region. The alga found at Ynyslas closely resembles Cotton's alga, but the position with regard to the tides is not identical. According to Cotton, the alga occurred in pure stretches or with scattered plants of *Glyceria maritima*, *Armeria maritima* or *Salicornia*, just above mean high tide level, so that it is submerged at the time of spring tides and may be dry for 9 or 10 days between them. At Ynyslas the fucoid community occurs at a considerably higher level, in the Juncetum zone (Fig. 2, XI), where, according to Yapp (**21**, p. 74), the substratum is only submerged during exceptional conditions of wind and tide, and presumably may be dry for many months at a stretch. As Yapp has shown, however (p. 70), the evaporating power of the air above the Armerietum is 2·26 times as great as that at a similar height (3 in.) above the substratum in the Juncetum zone, owing to the protection of the tall *Juncus* plants. No doubt, therefore, the shelter of the habitat at Ynyslas compensates to some extent for the rareness of tidal submergence.

The difficulty of identifying the Ynyslas plant accurately has already been referred to (see Part II, Carter (**6**), p. 206), and it is worth considering whether, in view of its higher position on the marsh, this alga may really be a form of *Pelvetia canaliculata*, and is possibly not identical with *Fucus vesiculosus* var. *muscoides* of Cotton, which has a lower vertical range. The normal form of *Pelvetia canaliculata* occupies a higher level on the seashore than *Fucus vesiculosus* (cf. Cotton (**8**), pp. 23, 52). It is possible therefore that both species have marsh forms, that of *Pelvetia* occupying a higher level than that of *Fucus*, and both occurring at a much higher level than their respective typical

forms. It is unfortunate that the marsh forms retain almost none of the distinctive characters of the typical form, so that these suggestions cannot be proved.

At Ynyslas the fucoid alga forms locally quite compact growths and there are few other algae associated with it. It may, however, sometimes possess a ground flora of *Vaucheria*.
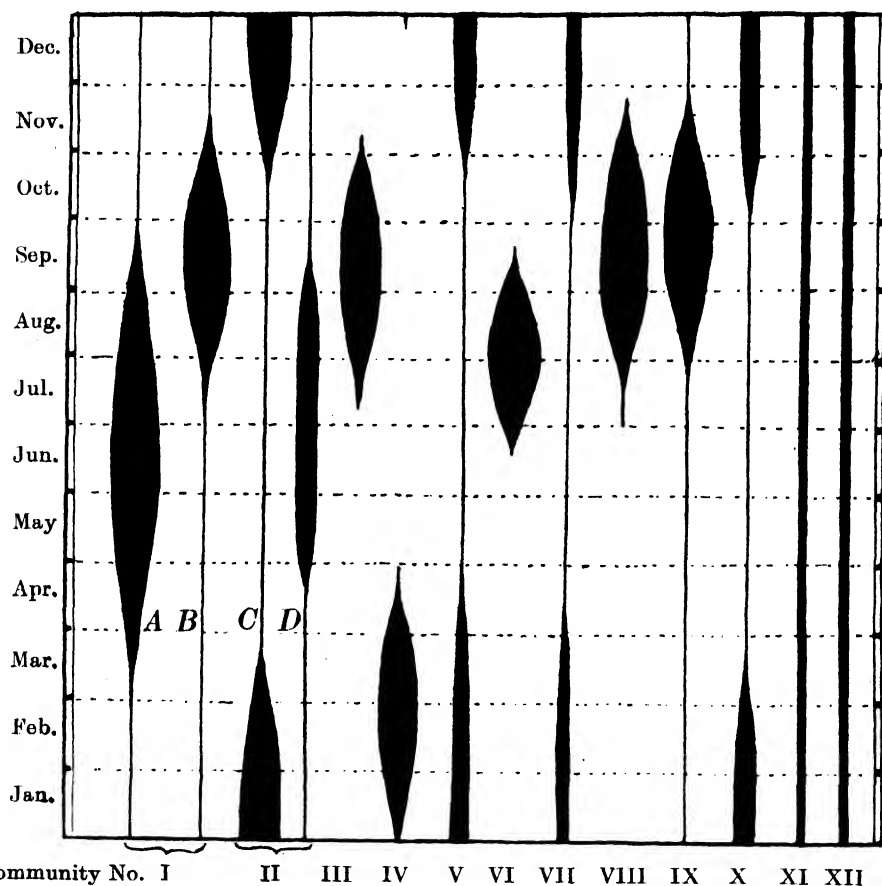
Fig. 3. Showing the seasonal periodicity of the algal communities of the salt marsh. I, general Chlorophyceae community; *A*, Chlorophyceae components; *B*, Cyanophyceae components, which become more prominent in the late summer and autumn. II, marginal community of diatoms; *C*, components with a winter maximum; *D*, components with a summer maximum. III, marginal Cyanophyceae community. IV, *Ulothrix flacca* community. V, *Enteromorpha minima-Rhizoclonium* community. VI, *Anabaena torulosa* community. VII, filamentous diatom community. VIII, autumn Cyanophyceae community. IX, *Phormidium autumnale* community. X, *Rivularia-Phaeococcus* community. XI, *Pelvetia canaliculata* ecad *muscoides* community. XII, *Catenella opuntia-Bostrychia scorpioides* community.

XII. Catenella opuntia-Bostrychia scorpioides *community.*

This community is represented all the year round (Fig. 3, XII). Cotton (**8**, p. 82) noted the association of these two plants, which he described as forming a pad under the rosettes of *Armeria maritima*, whilst in addition, *Bostrychia* hangs loosely from the branches of *Atriplex* or *Limonium*, along

channels. The distribution of these at Ynyslas and at Canvey has already been given (see Part II, Carter (**6**), p. 207), and it will be seen that there is much agreement with the facts given by Cotton. On the whole it is best to regard this community not as an independent one, but rather as an adjunct to the Juncetum zone at Ynyslas. *Bostrychia* as it occurs alone at Canvey can be considered as an adjunct to the *Obione* and *Glyceria* zones.

Some years ago (before 1926) a square foot of the Juncetum soil at Ynyslas was transplanted intact with its plants by Prof. Yapp into the Armerietum zone. In 1927–9 this transplant failed to yield any of the three larger algae, *Catenella*, *Bostrychia* and the fucoid. Unfortunately it is not known whether these algae were present originally in the transplant, before removal. Cotton states however (**8**, p. 82) that long exposure to air is important to the *Catenella-Bostrychia* vegetation. This is quite in accordance with its absence from the transplant in the Armerietum, which must have much more frequent submergence than the main Juncetum zone.

XI. Discussion.

Detailed ecological work on the algae of salt marshes is not abundant. Various investigators, working on the phanerogam flora of such regions have included scattered observations on the more obvious algal constituents (see Marsh (**16**), Walton (**19**), Morss (**17**)). Walton's paper on the Spitzbergen salt marsh is interesting since one of his pools contains quite a number of diatoms which have been observed in the present work. Apart from these papers dealing primarily with phanerogams, there have been investigations on particular salt marsh plants like those of Baker (**1, 2**) on the salt marsh Phaeophyceae; Conrad (**7**) on the Flagellates of brackish water; Gard (**10, 11**) and Bracher (**3, 4**) on *Euglena*. Gomont (**12**) gives a short list of salt marsh plants, but there is little detailed ecological work on salt marsh algae as a whole excepting that by Johnson and York (**14**) and Cotton (**8**). In his paper on the algae of Clare Island, Cotton confined his attention mainly to the larger forms, the smaller algae being as a rule neglected. A number of communities or "associations" were recognised, and besides those listed by him as salt marsh communities on p. 78, probably some others considered by him as part of the "sand and sandy mud formation" (p. 61) also come into consideration here. Thus a number of the communities described by Cotton in this paper can be recognised again in the alga vegetation of Ynyslas and Canvey, but in addition a number of other communities have been recognised of which no mention is made by Cotton.

Johnson and York (**14**) in their account of the vegetation of Cold Stream Harbour give useful information concerning some of the algae of brackish water, though their work embraced the flowering plants as well as cryptogams, and many of their determinations of the algae were only taken as far as the

genus. The area considered by them included some salt marsh, but the dominating phanerogam was in this case *Spartina*, a plant absent (except where planted) from both the areas studied in this work. These authors separated their plant communities primarily according to level, taking the mean low tide level as the basis of height, the high-tide level being 8 ft. higher. On the Welsh coast near Ynyslas, neap tides rise to 10 ft., and spring tides to 14 ft. 3 in., so that the range of the tides is greater there than at New York. In the Thames estuary the corresponding figures are 17 ft. 3 in. and 20 ft., so that here there is a still greater range coming under the influence of the tides. The mid-littoral belt (1·5–6·5 ft.) of Johnson and York and probably part of their upper littoral belt (6·5–8 ft.) as well, correspond to the areas of salt marsh studied at Canvey and at Ynyslas, although the levels are not comparable, owing to the difference in range of the tide. It is interesting to note that many of the same algae inhabit areas of salt marsh in the New World as in the Old, *Rhizoclonium, Vaucheria Thuretii, Enteromorpha* sp., *Lyngbya aestuarii*, and other algae frequently seen in the course of this work being also noted by Johnson and York. It is interesting too that they also speak of circular glistening patches of *Anabaena torulosa* which are so conspicuous at Canvey.

Johnson and York further state that of the twelve algae which are frequent in the upper littoral zone, among which are *Rhizoclonium riparium, Enteromorpha clathrata, Vaucheria, Microcoleus chthonoplastes* and *Lyngbya aestuarii*, any one of the twelve may grow by itself or with one or two others, or several may grow together as tangles. This corresponds quite well with the experience of the writer at Ynyslas. A growth of *Rivularia* on vertical overhanging banks was also noted by Johnson and York and is to be compared with the occurrence of a similar growth at Ynyslas. In the supra-littoral belt (8–12 ft.) Johnson and York only note amongst the algae the presence of *Lyngbya* sp. and *Nostoc* sp. This probably corresponds with the Upper Festucetum at Ynyslas. Diatoms were not given much attention by these authors, and there was no attempt to classify them according to level. Tide limits are given, however, for a number of species at the end of the work (p. 144) which, with a few exceptions, are quite consistent with the writer's observations. One notable exception is *Navicula Grevillii*, which certainly occurs in this country far higher than 1 ft. above mean low water; it has been observed in the *Glyceria* zone at Canvey which is not more than 1 or 2 ft. below high tide level.

The ecological study of salt marsh algae is difficult partly because they do not show sharp zonation with regard to level, and also because there is a definite periodicity according to the season of the year, the same piece of ground thus providing a substratum for several distinct algal communities which follow one another in regular succession as the seasons change. This is particularly striking at Canvey. At Ynyslas there is not the same conspicuous changing algal flora, because communities Nos. III, IV and VIII, which are the

markedly fleeting ones, do not occur there in their typical form, and No. VI is only occasional on the bare mud of channels.

It is in the *Aster-Salicornia* zone at Canvey, especially where the soil slopes down abruptly to the stretch of mud, that the most striking series of changes takes place. In December or the early part of the year a member of the Ectocarpaceae often appears, though not invariably. In January, about the same time, or soon afterwards, *Ulothrix flacca* develops, and covers up any pre-existing brown algae. Whether the brown alga is present or not, however, by February the soil and any remains of plants, such as *Aster* stumps, dead leaves, dead *Salicornia*, etc. are all completely enveloped by the *Ulothrix*. In March, this alga begins to decrease in vigour. Meanwhile *Enteromorpha* filaments make their appearance and by April or May have completely buried the *Ulothrix*. The *Enteromorpha* carpet lasts until about September, when the soil becomes bare or supports only Cyanophyceae except where *Vaucheria* is in possession. The dates given are of necessity only approximate, since the tides control the activity of the algae to some extent. A period of drought associated with a neap tide will tend to hasten the disappearance of many forms. The Cyanophyceae provide other, though less striking, examples of the same periodicity. Colonies of *Anabaena torulosa* appear almost spontaneously in July, their bright glistening colonies developing on the soil at the margins of the marsh, or on top of any algae which happen to be in possession of the substratum in the lower zones at that time.

The real ecological nature of this succession on the salt marsh is not very clear, and it is not easy to correlate it with any similar changes occurring in communities of higher plants. It is, of course, similar to the periodicity or succession of phases which is known to occur in the plankton of lakes and in the flora of ponds. Such periodicity is well established in the case of small algae living in an aquatic habitat; cf. West (20), Fritsch and Rich (9), Hodgetts (13). Probably this provides the nearest analogy to the series of events just described.

Amongst aerial plants, there is certainly some similarity to the seasonal phases of a woodland such as our familiar deciduous woodland, where the species most prominent in the herbaceous undergrowth change during the course of the year, some species having their most active phase in the spring and fruiting early, these being replaced by species whose period of activity occurs in the later months. The dominant plants of the woodland, the trees, are conspicuous throughout the year, but it is the periodicity of their activity which largely controls the changes in the subsidiary plants. Thus in a deciduous wood, the causes of the succession of phases in the ground flora, although immediately related to such conditions as light, can ultimately be traced back to the trees, and are therefore biotic in their origin.

Comparing the *Aster-Salicornia* zone at Canvey with such a woodland, the phanerogams, like the trees of the woodland, undergo seasonal changes. The

Aster plants are represented by a stump and basal rosette of leaves during the greater part of the year, and send up their tall flowering stems in late summer, but they are too distant from each other to affect seriously the illumination of the ground in the same way as the trees of the woodland. The cylindrical stems of *Salicornia* are only present from about May–October, and their peculiar morphology is such that they do not interfere very much with the ground flora of algae. Therefore the phanerogams of the *Aster-Salicornia* zone are probably not so largely instrumental in controlling the seasonal succession of algae clothing the soil, as the trees of a wood in determining the nature of the ground flora. The factors concerned on the salt marsh are probably not biotic but seasonal, such factors as temperature and moisture being most important, both rainfall and tidal submergence being included in the latter.

These seasonal changes in the salt marsh algae are most prominent in the *Aster-Salicornia* zone, because here the phanerogams are sparse, and do not impede the development of the algae. In the higher zones, such as the *Glyceria* zone, the flowering plants are more completely in possession, and the algae are not so abundant. Thus, although the alga flora is influenced by the same climatic factors as in the *Aster-Salicornia* zone, the biotic factors relating to the phanerogams tend to mask their effect, and the seasonal changes are not nearly as striking.

A seasonal succession which seems to be more analogous to that shown by the salt marsh algae in being controlled by seasonal or climatic factors is that described by Saxton (**18**), who studied communities of phanerogams succeeding one another seasonally on a low-lying piece of ground in India, where the vegetation showed conspicuous periodicity in relation to climatic changes associated with the monsoon. The changes in that particular case were very striking, since in the wet monsoon aquatics were predominant, these giving way, as drier conditions prevailed, to helophytes and grassland and eventually to xerophytic plants.

In contrast to deciduous woodland, where the herbaceous plants are affected largely by biotic factors, the vegetation described by Saxton, like the algae at Canvey, is controlled largely by climatic factors. Saxton found it difficult to analyse the vegetation of his area into associations, because, although some of the communities which appeared as phases in his area are known as stable communities elsewhere, in the region studied by him they were only transient and gave no lasting physiognomy to the area. Thus it seemed impossible to give them the status of association, and he accordingly suggested that the vegetation should be analysed into smaller units, *synusiae*, or communities of plants of the same life form. He therefore described the changing physiognomy of the area as being due to a succession of different synusiae. It does not seem possible to apply this method of analysis to the algal vegetation of the salt marsh. No one has yet suggested a system of life

forms for the algae, and in any case, the changing physiognomy in the succession of salt marsh algae is largely concerned with colour and texture, since the algae occurring in the different phases are nearly all of the same filamentous type.

<div align="center">(concluded)</div>

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TREE ROOTS AND THE FIELD LAYER

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(With three Figures in the Text.)

THE modern concept of forest implies relationships of varying intimacy between the members composing it, and the unravelling of these is an essential preliminary to the proper understanding of this complex plant community. In seeking to explain some of these relationships attention has chiefly been drawn to the influence of the tree canopy on the composition and vigour of the ground vegetation.

That light is a factor is not questioned. It acts directly on the field layer and also indirectly by setting limits to or stimulating soil processes, e.g. nitrification. But light as a direct factor has been invoked where it is not limiting, since the experiments of Fricke (2), Craib (1) and Watt (6, 7) show that on certain soils the restrictive influence on the field layer or certain constituents of the field layer is removed by cutting the tree roots. Fricke, and Craib, on the basis of moisture determinations of the soil concluded that the tree roots reduced the water supply below the limit for the field layer. Neither of these authors appears to have tested his conclusions by the artificial application of water. Moreover, "Hesselman has tried trenching experiments in Sweden with negative results" (Moore, 4). Thus, under certain conditions, neither light nor soil moisture may be limiting: in fact, the nature and vigour of the ground vegetation is conditioned by a complex of factors (5).

The experiments hitherto carried out do not therefore completely solve the problem. Many questions are left unanswered and it was our purpose to find satisfactory solutions to some of these by carrying out an experiment extending over several years. For various reasons it was found impossible to continue it and apart from occasional work in the third and fourth years it was practically abandoned after two years. The results obtained from this unfinished experiment are however considered of sufficient interest to justify publication, but it is hoped that the experiment will be repeated under more favourable conditions.

The experiment was designed to test Fricke's conclusions in the Heath Pinewoods of Aberdeenshire: to discover which (if any) plant nutrient or nutrients is limiting to the field layer: to find out in which soil layers competition between tree roots and the roots of the field layer takes place or is most severe: to test the validity of the concept that trees and the field layer are edaphically complementary and generally to discover the relation between the trees and the ground vegetation.

The area selected for experiment lies in a pinewood (*Pinus silvestris*) aged 65 years, with an average height of 62·5 ft. The woodland is in the *Deschampsia*

stage (**7**) with *D. flexuosa* dominant and *Oxalis acetosella* frequent to abundant, although somewhat patchy. *Galium saxatile, Goodyera repens, Luzula pilosa, Trientalis europaea* and *Vaccinium myrtillus* complete the list of species found on the plots. *Deschampsia, Oxalis* and the other species constitute 78, 15 and 7 per cent. respectively of the oven-dry weight of the original crops harvested (plots P_{1-7}).

The soil—a podsolised boulder clay—shows less marked podsolisation than in the type (**7**). The profile, dug to 24 in. shows the following horizons (Fig. 1 *a*).

Raw humus	2 in. (5 cm.)	Dark brown remains of *Deschampsia* and pine needles bedded and interwoven by living and dead roots of *Deschampsia*.
A_0	1·5 in. (4 cm.)	Slightly mineralised black peaty humus: greasy when wet, friable when dry.
A	2·5–3 in. (6·5–7·5 cm.)	Grey (A_2): humus stained above (A_1), dull brown below owing to humus deposition (A_3). No abrupt change to B or locally sharply demarcated by intense iron-humus deposition forming a pan-like zone.
B_1	8–11 in. (20–28 cm.)	Bright brown loose and friable soil of sandy loamy texture. Upper 4 in. (*a*) more ferruginous brown with darker humus patches associated with roots of pine and *Deschampsia*. These patches become more frequent in (*b*), then continuous below, forming a dull brown-red zone, abruptly changing to B_2 into which it passes in the form of cracks and locally of wider fissures.
B_2	At 15–18 in. (38–46 cm.) from surface	Greenish grey, little altered boulder clay. Superficial layer breaking up into angular fragments coated with dark brown humus-iron surface deposits. Thickness and continuity of these deposits diminish with depth.

The pine root system conforms to the "diffuse" type with the strongest roots spreading from the tree just inside the mineral soil or projecting partly into the black humus above. The obliquely descending roots are weaker and practically the whole of the root system lies above the B_2 horizon: a few roots penetrate cracks (Fig. 1 *c*).

The roots of *Deschampsia* (Fig. 1 *b*) are very abundant in the raw humus, becoming noticeably less so in A_0 but increasing again slightly in A_1. The rootlets then become less frequent with depth through B_1, until near the junction with B_2 they again become more richly branched, spreading horizontally. Roots also penetrate the superficial layers of B_2 and descend cracks to a depth of at least 24 in. from the surface of A_0. The humus patches in B_1 contain numerous rootlets, which often run alongside or near pine-roots.

The roots of *Oxalis acetosella* are quite superficial and restricted to the humus, with a maximum penetration of 2·5–3 in. (6·5–7·5 cm.).

The experiment was begun in September 1926. Plots 3 ft. × 3 ft. were selected, each with one side running as a tangent to the nearest tree and 3 ft. from it. Two plots P_1 and P_2 were left intact, and to P_2 2½ litres of distilled water were added periodically (on the average at 10-day intervals) during July and August, 1927 and from the end of April to the end of August, 1928. The amounts actually given work out at the rate of 27 in. and 20 in. per annum respectively. The average rainfall is about 32 in. Five more plots, P_3 to P_7, had trenches cut round them to different depths (Table I). During
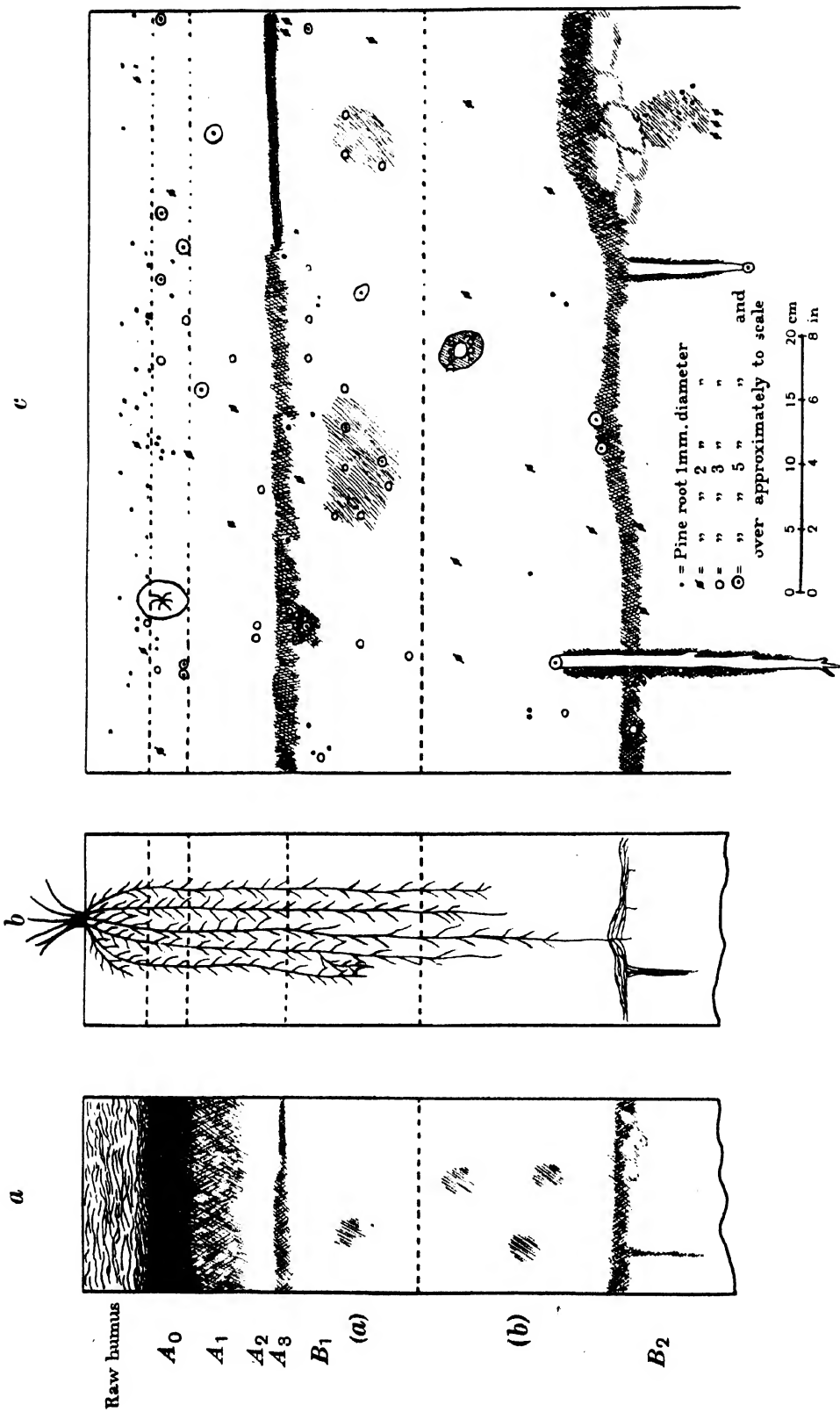
Fig. 1. *a*, Soil profile showing horizons; *b*, diagrammatic root distribution of *Deschampsia flexuosa*; and *c*, distribution of pine roots at 3 ft. from the stem. The depth of shading indicates the degree of humus and iron-humus concentration.

Table I. *Data of the plots under Pine, showing the effect on the field layer of the addition of distilled water, of nitrogenous manures, and of cutting the tree roots to different depths in the soil. All weights are in grams.*

No. of plot	Treatment	Species of the field layer	Weight of crop before cutting the roots Sept. 1926	Weight of crop one year after cutting the roots Sept. 1927		Weight of crop two years after cutting the roots Sept. 1928		Percentage N_2 (as NH_4) in oven-dry Deschampsia	Observations during 1927 and 1928
				Weight	Percentage increase or decrease on original crop	Weight	Percentage increase or decrease on original crop		
P_1	Control	Deschampsia flexuosa	6·35	2·16	−66	3·32	−48	2·092	Deschampsia sparse. Oxalis leaves subnormal in size. In 1927 Deschampsia had no flowering shoots: in 1928 it had two, of which one aborted
		Oxalis acetosella	1·55	0·70	−55	0·30	−81		
		Other species	0·36	0·10	—	0·09	—		
P_2	Distilled water added	Deschampsia flexuosa	8·18	1·74	−79	2·34	−71	1·986	Deschampsia sparse: no flowering shoots. Oxalis leaves as in P_1
		Oxalis acetosella	0·69	0·32	−54	0·27	−61		
		Other species	0·09	0·00	—	0·04	—		
P_3	Raw humus cut 1–2 in.	Deschampsia flexuosa	6·17	4·04	−34	4·09	−34	1·999	Deschampsia sparse: no flowering shoots. Oxalis leaves small
		Oxalis acetosella	1·12	0·82	−27	0·43	−61		
		Other species	1·86	0·12	—	0·06	—		
P_4	Raw humus cut, 3–4 in., to surface of mineral soil	Deschampsia flexuosa	6·95	1·98	−72	1·55	−78	1·544	Deschampsia and Oxalis as in P_3
		Oxalis acetosella	1·84	1·52	−17	0·72	−61		
		Other species	0·87	0·24	—	0·27	—		
P_5	Raw humus plus 4 in. mineral soil cut	Deschampsia flexuosa	7·14	7·96	+11	7·04	−1	2·721	Deschampsia showing same vigour as in woodland. In 1927 it had 3 flowering shoots; in 1928, 9. Oxalis dark-green and slightly larger leaves
		Oxalis acetosella	1·41	1·98	+40	1·39	0		
		Other species	0·05	0·00	—	0·06	—		
P_6	Raw humus plus 8 in. mineral soil cut	Deschampsia flexuosa	5·56	9·51	+71	8·02	+44	3·780	Deschampsia and Oxalis darker green and more vigorous than in woodland. Deschampsia had 5 and 16 flowering shoots in 1927 and 1928 respectively
		Oxalis acetosella	0·60	0·84	+42	1·70	+186		
		Other species	0·70	0·12	—	0·23	—		
P_7	Raw humus plus 13–18 in. mineral soil cut	Deschampsia flexuosa	7·03	11·41	+62	14·07	+100	3·218	Deschampsia distinctly darker green and Deschampsia and Oxalis very vigorous. In 1927 Deschampsia had 7 flowering shoots, but all aborted: in 1928, 7, of which 4 aborted
		Oxalis acetosella	1·80	1·85	+3	2·12	+18		
		Other species	0·53	0·00	—	0·01	—		
P_8	$NH_4.NO_3$ applied at a rate equal to 1 cwt. $(NH_4)_2SO_4$ per acre	Deschampsia flexuosa	7·78	—	—	10·04	+29	—	In 1928, Deschampsia had no flowering shoots
		Oxalis acetosella	0·75	—	—	0·37	−51		
		Other species	0·21	—	—	0·21	—		
P_9	$NH_4.NO_3$ at a rate equal to 2 cwts. $(NH_4)_2SO_4$ per acre	Deschampsia flexuosa	8·34	—	—	11·74	+41	—	In 1927, Deschampsia had 2 flowering shoots
		Oxalis acetosella	0·98	—	—	0·38	−61		
		Other species	0·01	—	—	0·00	—		
P_{10}	$NH_4.NO_3$ at a rate equal to 4 cwts. $(NH_4)_2SO_4$ per acre	Deschampsia flexuosa	11·80	—	—	9·68	−18	—	Deschampsia had no flowering stems. Oxalis disappeared
		Oxalis acetosella	0·56	—	—	0·00	−100		
		Other species	2·34	—	—	1·07	—		
P_{11}	$(NH_4)_2SO_4$ at the rate of 2 cwts. per acre	Deschampsia flexuosa	9·57	—	—	6·36	−34	—	Deschampsia had 3 flowering stems. Oxalis disappeared. This plot remained the poorest throughout 1927 and 1928
		Oxalis acetosella	0·56	—	—	0·00	−100		
		Other species	0·86	—	—	0·14	—		

the opening of the trench the soil taken out was put on a waterproof cover, thus avoiding any effect due to mixing mineral soil with the raw humus. To avoid "edge effect" smaller plots, 2 ft. × 1 ft. inside the larger were permanently staked for record. The vegetation on these smaller plots was harvested in September 1926 before cutting the trenches and harvested again in September 1927 and September, 1928. The crops were dried first in an incubator and then in an electric oven at 95° C. until the weights remained constant within 1 per cent. The weighings were made to 4 decimal places,
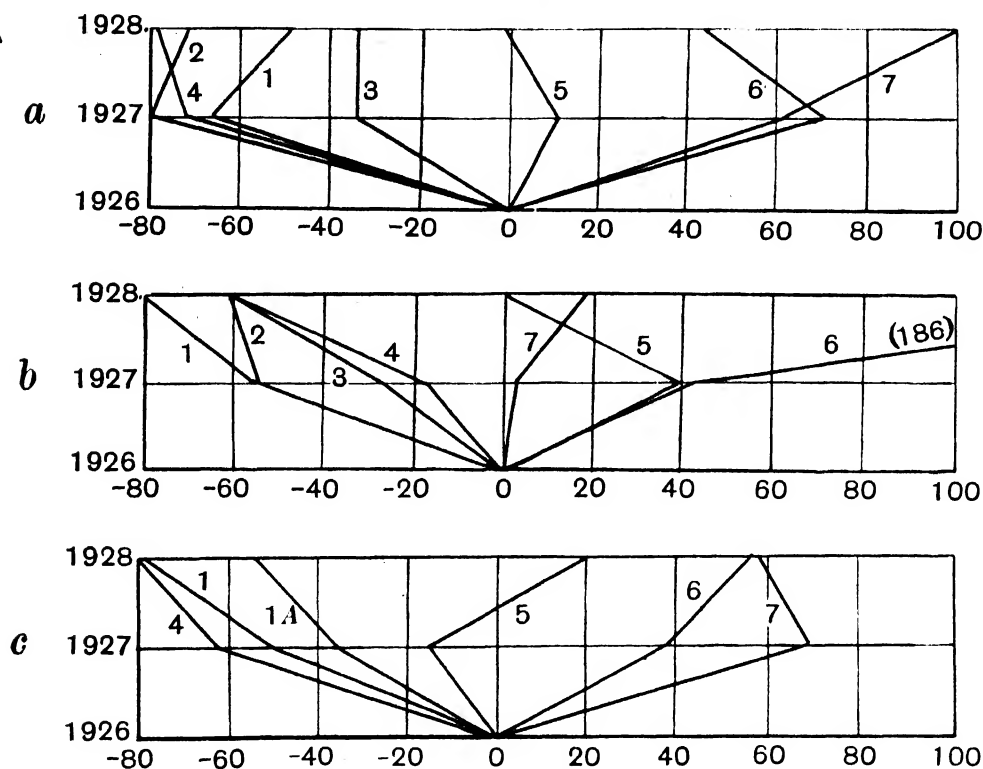
Fig. 2. Graphs of data for plots P_{1-7} in Tables I and II, showing percentage increase or decrease in the weights of the original crops after watering and cutting pine and beech roots to different depths. *a, Deschampsia flexuosa* in pine plots (*P*). *b, Oxalis acetosella* in pine plots (*P*). *c, Oxalis acetosella* in beech plots (*F*).

although only two are given in the table. The crop weights are also calculated as a percentage increase or decrease on the *original* crop in each plot (Table I and Fig. 2 *a* and *b*).

To four additional untrenched plots (P_8–P_{11}) nitrogenous manures were added in one dose on May 22nd, 1927 and repeated on May 21st, 1928.

Since rabbits grazed the *Deschampsia* on the manured plots the whole experiment was fenced in at the beginning of April 1928.

Beside this experimental area stands an old beech of pioneer form. Below it the litter and humus is 4 in. thick and *Oxalis* is frequent to abundant. The

beech root system is diffuse, with a definite concentration of larger roots between the litter and the mineral soil. Six plots, 2 ft. × 1 ft., end on to the bole and equidistant 8 ft. from it, were laid out. Two (F_1 and F_{1A}) were left as controls: four (F_4 to F_7) had trenches cut round them to different depths at about 6 in. from the margin. The same precautions were taken as before and the crops dealt with in the same way (Table II and Fig. 2 c). In this series no plot was watered or manured.
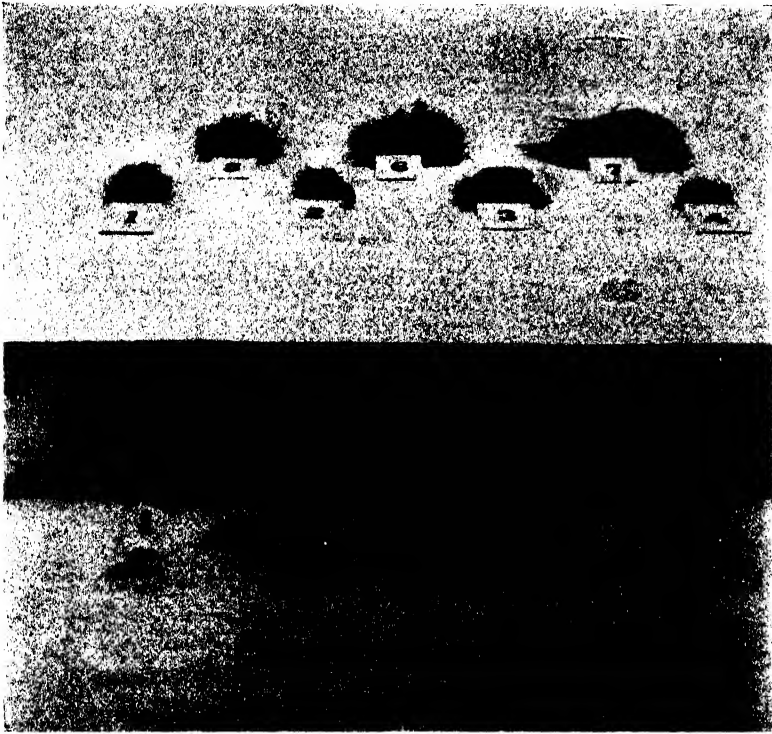
Fig. 3. The crops of *Deschampsia flexuosa* (upper photo.) and of *Oxalis acetosella* (lower) from the Pine plots 1–7, Sept. 1928, two years after cutting the tree roots. Note the increase in size of crop with increasing depth of cut: the effect is seen both in the deep rooting *Deschampsia* and the shallow rooting *Oxalis*.

During the first two years of the experiment the plots were visited, about once a week, during the vegetative season and at irregular and longer intervals during the winter. Records were kept of the vigour of the crops and of the number of flowering shoots on each plot. A satisfactory picture of the relative vigours of the crops may be obtained from the data and from the photographs (Fig. 3). Notes on the flowering are given in the last column of Table I.

The results cannot be subjected to statistical treatment. It was expected that variations and the experimental error in cropping would smooth themselves out in time, but the abrupt termination of the experiment precludes this hope. In drawing conclusions from data which are very suggestive and

Table II. *Data from the plots under Beech showing the effects on the field layer of cutting the tree roots to different depths in the soil. All weights are in grams.*

No. of plot	Treatment	Species of the field layer	Weight of crop before cutting the roots Sept. 1926	Weight of crop one year after cutting the roots Sept. 1927		Weight of crop two years after cutting the roots Sept. 1928		Observations during 1927 and 1928
				Weight	Percentage increase or decrease on original crop	Weight	Percentage increase or decrease on original crop	
F_1	Control	Oxalis acetosella	0·47	0·23	−50	0·10	−79	Normal
		Deschampsia flexuosa Vaccinium myrtillus	0·30	0·07	−76	0·01	−95	
F_{1a}	Control	Oxalis acetosella	0·44	0·28	−36	0·20	−54	Normal
		Deschampsia flexuosa Vaccinium myrtillus	0·23	0·05	−80	0·01	−96	
F_4	4 in. litter cut to mineral soil	Oxalis acetosella	0·26	0·10	−62	0·05	−80	Rather poor plot
		Deschampsia flexuosa Vaccinium myrtillus	0·20	0·04	−85	0·003	−99	
F_5	Litter cut, plus 4 in. mineral soil	Oxalis acetosella	0·32	0·27	−15	0·38	+20	Oxalis darker green with larger leaves. In Sept. 1927 when harvested many leaves were missing, but stalks left: the leaves were present 7 days before
		Vaccinium myrtillus	0·08	0·01	−88	0·01	−88	
F_6	Litter cut, plus 8 in. mineral soil	Oxalis acetosella	0·27	0·37	+38	0·43	+57	Oxalis darker green with larger leaves
		Vaccinium myrtillus	0·003	0·00	−100	0·00	−100	
F_7	Litter cut, plus 12 in. mineral soil	Oxalis acetosella	0·22	0·38	+70	0·35	+58	Oxalis darker green
		Deschampsia flexuosa Vaccinium myrtillus	0·26	0·17	−35	0·004	−99	

lend themselves to much speculation the authors have confined themselves to what appear legitimate deductions. They wish neither to be dogmatic nor timid in offering their interpretation as something more than accredited suggestion with the stamp of high probability.

GENERAL DEDUCTIONS.

The assumption is implied that, at the time of laying down the experiment, the vegetation of each plot had reached a stable equilibrium with its environment.

In assessing the effect of the different treatments account must be taken of the diminution in the size of the crops due to harvesting. In this respect *Oxalis* suffers more than *Deschampsia* (a somewhat unexpected result), for while in the second year *Deschampsia* holds its own, *Oxalis* shows a further decline (Fig. 2, graphs P_1, P_2, P_3, P_4 and F_1, F_{14}, F_4). The other species are present in too small amounts to justify any conclusion being drawn.

The addition of distilled water on the surface is without effect on *Deschampsia* or *Oxalis* (Fig. 2 *a* and *b*, graphs 2).

A scrutiny of the graphs shows that the effect of cropping is not overcome by any cutting down to the mineral soil: that cutting through the humus and 4 in. of the mineral soil (and the chief pine and beech roots) enables both *Deschampsia* and *Oxalis* to hold their own (graphs 5), so that in the absence of harvesting the crop would have benefited to some extent by the changes due to trenching: and that both *Deschampsia* and *Oxalis* benefit greatly by trenching to the deeper soil layers. The graph for *Oxalis* (Fig. 2 *b*, 7) is an exception, but reference to the data shows that the absolute size of the crop was the largest of any. Competition between *Deschampsia* and *Oxalis* may be suggested and while in P_6 a decrease in the *Deschampsia* from $+ 71$ to $+ 44$ is accompanied by a great increase in *Oxalis* there is scarcely enough evidence to conclude that the continued increase in *Deschampsia* in P_7 accounts for the small increase in *Oxalis*. It is probable however that the deepest trench favours the *Deschampsia* relatively to the *Oxalis*. A favourable influence of *Deschampsia* on *Oxalis* is excluded as a possible factor because corresponding increases in *Oxalis* are found in the beech plots—at any rate up to the 8 in. trench (F_6).

Differences in the flowering of *Deschampsia* were pronounced. In the woodland generally flowering was sparse and no significant departure from this behaviour is met with except in P_5, P_6 and P_7, where in 1928 there appeared 9, 16 and 7 flowering shoots respectively. Further, in P_5 all 9 survived till September 1928 whilst 15 survived in P_6 and only 3 in P_7. Conditions for flowering are evidently most favourable in P_6 and while the absolute crop in P_7 is almost double that of P_6 yet conditions are less suitable for flower production.

In January, 1932, a profile was exposed through plot P_7. The humus zone (A_3) is much more diffuse and the B_1 horizon more loose and friable than outside the plot. *Deschampsia* roots are much more abundant to a depth of 5 in. and richer throughout B_1, but especially so round the plot margin, i.e. near the trench, where they are also abundant to a greater depth. The friability of the soil is not a local variation but is a result of cutting the trench and possibly directly due to the root action of *Deschampsia*. But this requires further study.

<center>DISCUSSION.</center>

It is commonly stated that trees and their accompanying herbs are edaphically complementary. This conclusion is based on the distribution of the roots alone and takes no account of (1) the part played by the tree roots at different layers to supply water and nutrients to the tree and (2) the effect of the lower soil layers on shallow rooting plants. Thus Scandinavian authors (e.g. Lindquist (3)) claim that there is no correlation between tree growth and the herbaceous vegetation because tree roots tap soil layers too remote to affect the herbs. But if, as is sometimes stated—and there is ground for the belief— the bulk of the nutrients supplied to the tree comes from the surface layers and the deeper roots provide little else but water, then both herb and tree are exploiting the same layer for nutrients, the difference being that whereas the tree is not dependent on the superficial soil layers for water the herb presumably is.

Now *Deschampsia flexuosa* is a deep rooting grass and *Oxalis acetosella* is a shallow rooting herb. On the commonly accepted hypothesis *Deschampsia* and *Oxalis* would compete with the tree roots at all depths up to the limits of their root penetration, but the evidence from this experiment shows that cutting the roots below the limit of penetration of *Oxalis* has a progressively beneficial effect at least up to 8 in. from the surface of the mineral soil, and that the maximum increase in *Deschampsia* is obtained (after two years) by cutting to at least 13–18 in. from the same level.

At the start of the experiment it was thought that cutting the main tree roots running at or near the mineral soil surface would produce the maximum effect at any rate on *Oxalis*, but the data in both the pine and beech plots show that the gain is just sufficient to offset the handicap of cropping. Cutting down to the mineral soil does not of course interfere with the rootlets (except near the margin of the plot) rising upwards from the main roots into the humus. Thus the absence of an effect due to cutting to this depth may be explained on the ground that pine root competition is not really removed from the stratum occupied by the roots of *Oxalis*. But the progressive benefit accruing from trenching to lower levels shows that the deeper lying roots or soil layers have some influence on the *Oxalis* roots lying in the humus.

In the absence of a complete record of the factors affecting the growth of *Deschampsia* and *Oxalis* in the plots it is impossible to separate effects on the crop due to the removal of tree root competition and to changes (e.g. decay of roots) following cutting. Water applied on the surface did not have any effect. It is possible however that the water applied did not reach the lower soil layers, but the absence of a definite effect on *Oxalis*, which would clearly be exposed to the addition, renders unlikely the hypothesis that water is the limiting factor. It is still possible however that *Deschampsia* may benefit from water applied at a suitable depth in the soil. To test this wax lined holes $\frac{1}{2}$ in. in diameter were formed and water applied (during 1929 and 1930) at 4 in. and 8 in. from the mineral soil surface in plots P_1 and P_2 respectively. The resulting crops were not harvested and the qualitative assessment in the field puts the two plots watered in this way just better than plots P_3 and P_4 in 1929 but similar to them in 1930. All four remained poor and distinctly poorer than the plots where the mineral soil was cut.

As a factor contributing to enhanced vigour, improved soil aeration would appear to be dismissed on the ground that the cropped part was in the centre of the area round which the trench was dug and because in one plot surrounded by a deep trench the vigour of *Deschampsia* and *Oxalis* shows a sharp transition on the side next the tree whose roots were cut and a gradual change on the side remote from it. The effect in this case therefore does not appear to be an extension from the trench. Nevertheless the possibility remains that soil aeration is improved by the decay of the severed roots: and the further possibility exists that trenching affects the internal drainage system of the trenched plots and with it the soil aeration. A distinction must thus be made between a possible effect due to disturbance of the water-air-soil system as the result of trenching and an effect due to the removal of root competition. The position is further complicated by the repercussion on the soil of the enrichment of the *Deschampsia* root system to lower levels.

The deeper pure green of the crop inside P_5, P_6 and P_7 suggests an increase in the nitrogen available. Determinations of the percentage of total nitrogen contained in the 1927 crop of *Deschampsia* are given in Table 1. The data are remarkably uniform for P_1, P_2 and P_3 and show a definite increase in P_5, P_6 and P_7 with a maximum in P_6. In view of Lindquist's statement that *Deschampsia flexuosa* is a mycotrophic plant dependent for survival on the absence or restriction of nitrification, it is assumed that no nitrification was taking place. But it would have been of interest to find out exactly what conditions restricted flowering, while promoting vegetative growth. To test the hypothesis that nitrogen is a limiting factor doses of nitrogenous manures were applied (Table I, P_8–P_{11}). The results of the first year were nullified because rabbits ate the manured grass. (It is significant that in a previous experiment where the tree roots were cut, rabbits definitely preferred the *Deschampsia* inside the plot.) The results from 1928 show that the application

of limited doses of ammonium nitrate had a beneficial effect on the *Deschampsia* but the largest dose as well as the application of ammonium sulphate had an adverse effect. On *Oxalis* the effect is more striking: the two smaller doses of ammonium nitrate had no stimulating effect while the application of ammonium sulphate and the largest dose of ammonium nitrate eliminated *Oxalis* altogether. The application of the nitrogen produced a colour change somewhat similar (but a bluish green rather than a pure green) to that in the trenched plots P_5-P_7, but the final judgment in the field is that the physiological effect is not the same. It is possible that the same application spread over a period may yield different results. One may however conclude from the evidence that increased availability of nitrogen is in all probability one factor responsible for the increase in *Deschampsia*. Whether the increase of nitrogen is due to the removal of the tree roots as competitors or to changes following trenching is not determined.

While this experiment is incomplete it directs attention to the changes in the physical condition of the soil in the plot brought about by cutting a trench round it. It also opens up the whole question of the relationship between the trees in a woodland and the accompanying herbs and grasses, and points to the need of examining afresh the concept of edaphically complementary species. Just as the tree layer affects the light intensity at the level of the field layer so it appears that deeper lying tree roots may not be without influence on the welfare of the plants whose roots are restricted to the surface layers of the soil.

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PLEISTOCENE CLIMATIC CHANGES AND THE DISTRI-BUTION OF LIFE IN EAST AFRICA

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(With one Map in the Text.)

INTRODUCTION.

No study of the distribution and ecology of living things can be made without the question arising how the present state of affairs became established. I have been brought to consider this problem in East Africa as an ornithologist with no qualification to deal with forms of life other than birds. But it will be obvious that any argument developed must be much concerned with botanical facts, and that any conclusions reached must be applicable to the distribution of animals in general and of plants as well[1]. It is for this reason that the title of the present paper is in wide terms, although the examples I shall use are mainly avian[2]. The fact that they are drawn from the most potentially mobile class of living things does not lessen their cogency. Every naturalist with field experience would agree that owing to their specialised ecology birds such as those that will be cited provide data no less acceptable for the present discussion than would a skink or a potto. Thus Chapman (1926) out of his immense experience of Andean bird distribution remarks: "There may be cases of discontinuous distribution...which are due to accidental dispersion, but, in my opinion, they are too rare to have any bearing on the general problem."

The distribution of species in East Africa raises several general problems for which no explanation can be derived from a study of the present-day conditions.

(i) Chief among them is the similarity of the fauna and flora of the mountains, a similarity that extends to all the peaks of Tropical Africa, the characteristic montane forms being wholly absent from the hundreds of miles of intervening country (cf. Bannerman (1930), pp. xl-xlii). Most of the birds

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[1] I wish at the outset to express my indebtedness to Mr P. J. Greenway, Botanist at the East African Agricultural Research Station, for help in his special subject; to Mr T. W. Kirkpatrick, also of the Research Station, for valuable criticism; and to Mr C. Gillman, Chief Engineer of the Tanganyika Railways, for guidance in geological matters.

[2] For distribution in Africa generally from **Sclater** (1930), whose work provides a conspectus of the African Aves particularly apt for this purpose and not, so far as I am aware, paralleled in the literature of other classes of animals. Some of the East African data are drawn from personal observations, publication of which has been begun (**Sclater** and **Moreau**, *Ibis*, 1932, pp. 487–522, being the first of five parts).

concerned are closely associated with the montane forests, which are tall, closed, mainly evergreen communities. Indeed, as will be described later, the present physical condition of East Africa is such that, unlike West Africa, there is practically no forest of this type anywhere except on the mountains, and therefore a "forest species" nearly always connotes a montane habitat. Of this class *Heterotrogon vittatum* (Shelley), *Turdus olivaceus* Shelley, *Chlorophoneus nigrifrons* Rchw., *Onychognathus walleri* (Shelley), *Cryptospiza salvadorii* Rchw. may be quoted among many others, as being represented in one form or another, in practically every forest on the accompanying map[1] (Fig. 1). Typical examples of widespread but discontinuous distribution are afforded by *Seicercus ruficapilla* (Sundev.) from Nyasaland and the Usambaras, and *Cercococcyx montanus* Chapin, known only from Ruwenzori, Usambara and Uluguru. Some of the forest species in question live in the canopy, e.g. *Heterotrogon*, some in the intermediate strata of vegetation, e.g. *Trococercus albonotatus* Sharpe, and others, e.g. *Sheppardia cyornithopsis* Sharpe, hardly leave the thickly shadowed ground. All are bound by the closest ecological ties to the montane forests by a complex of factors which doubtless vary from species to species. The subject is a particularly difficult one that awaits critical investigation. A preliminary attempt to deal with it is being made by the writer in the Usambara Mountains, and the experience gained only deepens the impressions received from a study of the recorded distribution of the forms concerned that they disappear entirely *pari passu* with forest, and that their movement from one locality to another is only possible when a connection of forest exists. At the same time, a belt of forest may act as a barrier to the dispersal of non-forest birds. Generally speaking, a forest form seems quite incapable of adapting itself to life in any other association, even though, in an epoch like the present, when forests are progressively diminishing in area, the "economic pressure" on the birds within its limits must be strong. The converse is equally true. This is well illustrated in West Africa by Bates' recent study of differentiation (1931): the number of species represented both within and without the forest, even in different forms, is negligible compared with the long list of those entirely confined to the forest and often racially differentiated within its limits.

A few of the mountain birds are, however, associated not with the forests but with the open country above the timber line. Such are *Nectarinia johnstoni* Shelley and *Pinarochroa sordida* (Rüpp.), the first from Nyasaland to Mount Kenya, but nowhere below 8000 ft., and the second from Abyssinia to Kilimanjaro where the peaks exceed 10,000 ft.

(ii) Marked affinities with West Africa are found, among vertebrates generally, within sight of the Indian Ocean (cf. *Carnegie Institution Year Book*, No. 29, 1929–30, p. 359), and they appear to be at least as strong in the Usambaras and Ulugurus as anywhere east of Victoria Nyanza. Among birds,

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[1] I am indebted to Mr F. J. Nutman for redrawing the map.

the genera *Neocossyphus* and *Hyliota*, the species *Lampribis olivacea* Dubus., *Anthreptes tephrolaema* (Jard. and Fras.), *Illadopsis rufipennis* (Sharpe), *Bubo poensis* Fraser and *Gypohierax angolensis* (Gmel.), may be quoted. Mammalian examples are afforded by *Crocidura maurisca geata* Allen and Lov. and *Otomys Kempi* Dollman (Allen and Loveridge, 1927). Among forest trees *Tylostemon Kweo* Mildb., *Englerodendron usambarense* Harms, *Schefflerodendron usambarense* Harms, *Anisophyllea laurina* R.Br., *Crotonogynopsis usambarica* Pax, are all forms of West African affinity making their appearance on the east side of the continent only in Usambara and Uluguru.

(iii) Connected with the wide but discontinuous ranges of the montane birds is the fact that most of the species have become differentiated into a number of races. It will suffice to quote as examples *Linurgus kilimensis* (Rchw. and Neum.), represented by the typical form on Kilimanjaro and by *L. k. elgonensis* v. Som., *L. k. keniensis* v. Som., and *L. k. rungwensis* Bangs and Lov., on the mountains that have given their names to the respective subspecies, and *Apalis r. ruficeps* Rchw. from the Usambaras with *A. r. altus* Friedm. from the Ulugurus. There can be little doubt that such races, especially those in close geographical proximity, were differentiated in isolation, and it becomes of interest to determine for what period of time the isolation has been effective.

(iv) Within the closed forest itself, which imposes approximate homogeneity in certain of the most important environmental factors, the bird fauna shows a definite zonation by altitude. This can nowhere be studied so well as in the Usambara Mountains, for there alone in the whole of East Africa is a practically unbroken series of forest available for observation down to within 500 ft. of sea-level. Careful examination has made it clear that a whole fauna, including representatives of such species as *Trococercus albonotatus* Sharpe, *Geokichla gurneyi* (Hartl.), *Turdus olivaceus* Linn., *Chlorophoneus nigrifrons* Rchw., *Turturoena delegorguei* (Del.), *Mesopicos griseocephalus* (Bodd.), *Alethe fülliborni* Rchw., *Alseonax minimus* (Heugl.), occupies the forest at 3000 ft. and is unknown at 2000 ft.[1] This may be called the subtropical fauna. A few species, e.g. *Apalis thoracica* (Shaw and Nodd.) seem to have their lower limit at about 4000 ft. and several, comprising a "temperate" fauna, e.g. *Laniarius fülliborni* (Rchw.), *Alethe anomala* Shelley, *Cinnyris mediocris* Shelley, *Arizelocichla nigriceps* (Shelley), *Pseudoalcippe abyssinicus* (Rüpp.), *Pholia* spp., all birds of the same fundamentally homogeneous closed forest, do not descend appreciably below 5000 ft. I believe that no comparative study of bird-zonation on African mountains has been published, but such information as is available about the limits of these species on the various mountain masses where they are represented, warrants the belief that their altitudinal relations to each other are constant. How these altitude limits exert their influence

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[1] It may be noted that owing to the peculiar local conditions 3000 ft. in the East Usambaras corresponds climatically to 5000 ft. in some more inland situations.

on the organism is uncertain. It is, however, significant that some of the subtropical species flourish at sea-level in South Africa. In any case, it is clear that within the belt of mountain forests we have to deal with certainly two distinct faunae. The upper, "temperate," fauna is as widely, and even more discontinuously, distributed at the present day than the "subtropical." While the various faunal islands of "subtropical" forest are isolated from each other by non-forested areas, the "temperate" faunal islands are separated by the further barrier of the subtropical zone on every mountain where the "temperate" fauna occurs.

It is important to observe that the fauna of each zone is almost exclusively composed of *species* different from those of the contiguous zone, not merely of different races. In other words, there is no close phylogenetic relation between the faunae. It is therefore improbable that one was derived from another, even if parallel evolution on each of the isolated mountain masses were conceivable. The possibility suggests itself that the subtropical and temperate faunae were "laid down," to use a geological simile, at different epochs.

Until very recently no serious attempt was made to attack these four problems. Indeed I do not think the existence of the last one has been fully realised. Reichenow (1900) suggested that the mountains might once have formed an archipelago in the sea, all the intervening lowland being covered, and that their inhabitants had never succeeded in expanding beyond the narrow limits within which they were then confined. This hypothesis was, of course, unsupported by any geological evidence, all the facts indicating that continental Africa is a land-mass that has not been submerged since very remote geological times. Most students have preferred to postulate "climatic charges," which for years were advanced, so far as zoologists are concerned, as merely unsupported speculation. I am indebted to Mr Gillman for references which show that the German geologists (e.g. Meyer, Dantz, Uhlig, Kuntz, Jaeger) gave repeated testimony to the former existence of a pluvial. As early as 1900 Meyer published evidence of former more extensive glaciation on Kilimanjaro. The Ruwenzori evidence was even more striking: "Die ersten unzweifelhaften Beweise für die alte Vergletscherung...fand ich bei dem Abhänge von Bihunga, d. h. in einer Höhe von ungefähr 1500 Meter[1], während gegenwärtig die Gletschen nicht tiefer als bis 4200 Meter herabreichen" (Savoyen, 1909, p. 448). For some reason the zoologists seem to have been less familiar with the results obtained by these German workers than the botanists were. Writing in 1923 Chapin could only observe: "probably there were changes of topography and climate in the past which permitted extension of the mountain floral zones." So recently as 1928 Stresemann and Grote, seeking to adduce evidence of a former extension of closed forest in Equatorial

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[1] **Nilsson** (1929, p. 256) on subsequent examination put the lower limit of past glaciation at 2000 instead of 1500 metres.

Africa, rely on the evidence of (then) indefinitely established pluvials in Egypt and South-west Africa, and quote Lönnberg's conclusion that it was "wohl wahrscheinlich dass auch das dazwischenliegende Land etwas ähnliches durchgemacht haben dürfte."

At last in 1929 came Lönnberg's important contribution to the problem, in which he was able to rely on Nilsson's conclusions (1929) from local geological evidence, that East Africa had witnessed not merely a single pluvial, but a succession of pluvials[1]. The last two years have seen the publication of several papers (Wayland, 1930 and 1931; Leakey, 1930 and 1931[2]) that confirm and amplify Nilsson's conclusions to a point where it appears to me that we can now estimate, with some approach to definition, the possible effect of the climatic alternations on animal distribution and the relative remoteness in time of the important changes. The conclusions reached in this discussion must be highly tentative. I cannot emphasise this too strongly, for it is not to be supposed that the last word has by any means been said on the geological premises themselves. But I feel that this paper will be justified if it helps to bring into focus the prehistoric background, hitherto absent or only adumbrated, against which any question of distribution must be viewed.

It is obvious that the key to the whole problem lies in the expansion and contraction of closed forest of one type or another. Whether the forest is completely evergreen or to some extent semi-deciduous does not seem to be important so long as it is a tall closed association that does not lose a considerable proportion of its leaves at any particular season[3]. It is proposed, then, to describe briefly the present conditions in East Africa; to give an indication of the limits of rainfall and temperature for the existing forest types; and so to obtain some idea of the climatic conditions that would be needed to bring the isolated forests of the present day into connection. The geological evidence for climatic fluctuations will then be summarised, and an attempt made to interpret the maxima and minima in terms of forest extension.

PRESENT CONDITIONS.

But little of the interior of East Africa lies appreciably below the altitude of 4000 ft. and except for the Nile basin its present aspect is primarily that of an arid savannah tending in the north-east towards desert. It is, however, narrowly edged on the coast with a more humid zone, and at comparatively

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[1] I wish to express my thanks to Dr Lönnberg for his kindness in supplying me with separates of his own and Nilsson's papers.

[2] I have not had an opportunity of perusing Dr Leakey's paper given before the British Association in 1930; but I have to thank Dr C. E. P. Brooks for an extract from it, and also for aid in interpreting the results recorded.

[3] Many of the most characteristic forest species, such as *Chlorophoneus nigrifrons* Rchw., *Cryptospiza salvadori* Rchw., *Alethe poliocephala kikuyuensis* Jacks., are recorded from Nairobi, where the forests are, according to Troup, semi-deciduous.

wide intervals it bears upon its surface patches of closed forest, of many different types, but almost without exception confined to the highest ground.

The accompanying map is compiled, so far as the Kenya and Uganda Forests are concerned, from Troup's two reports (1922), and for Tanganyika from Meyer (1909) and local knowledge. The rainfall data are derived from Knox (1911)[1], Kendrew (1927), Sayers (1930), and Plate XXII of the *Meteorological Maps of the Atlas of Egypt* (1928), which supplement each other and differ in details. The small scale unfortunately makes it impossible to show more than two contours, the 3000 ft. and 6000 ft., and two isohyets, for 30 in. and 40 in. rainfalls.

It will be seen that over practically the whole of Central Tanganyika Territory and the greater part of Kenya Colony the rainfall is under 30 in. a year. The Kenya Highlands themselves are cleft by a wedge of arid country, for the rainfall in the Rift Valley as a whole does not exceed that figure. In the catchment of Lake Nakuru, which will be frequently referred to later in this paper, it reaches 37·5 in., as calculated from the averages over a number of years given in the *Summary of Rainfall in Kenya Colony*, 1930 (B.E.A. Meteorological Service), for five local stations. The ill-effects of this generally scanty rainfall in the interior are aggravated by its bad distribution. Practically the whole of it falls in two short seasons of the year, which tend, as one travels south from the Equator, to merge into one. The effect on the vegetation is to make it impossible for any to exist that is not deciduous or xerophytic: and the overwhelmingly greater part of the East African interior is therefore occupied by grass-, thorn-, or bush-steppe, and more or less open Miombo (*Berlinia-Brachystegia*) woodland. During the dry season fires rage over this type of country, and what with the leafless condition of the trees and the scantiness of the ground cover, diurnal animals can only exist if they are at home in the full glare of the tropical sun.

Within the Nile basin the precipitation is nowhere less than 40 in., generally well-distributed under the influence of the extensive lakes and swamps: and much of the Uganda Protectorate receives nearly 60 in.

The coastal belt is also somewhat more favoured than the interior, with a rainfall exceeding 40 in. and rising opposite Pemba Island to 60 in. On the whole, moreover, it is in this belt better distributed than inland, and the prevailing winds are less desiccating than those of the interior. These conditions support along the coast a more or less deciduous bush with patches, totalling perhaps 20 square miles in Kenya Colony, of closed though not tall forest[2]. Where the eastern edge of the interior plateau faces the Indian Ocean,

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[1] His Pl. I inevitably suffers from its scale. The 70–80 in. rainfall islands of the Usambaras, Ngurus and Ulugurus cannot be shown.

[2] **Troup** (1922, p. 5) gives the Arabuko "Forest Area" as 132 square miles, but much of this is *Brachystegia* woodland (Mr R. M. Graham *in litt.*) and **Hutchins** (1909) in his map appends a note to what he calls the "Arabuko and Sekoki Forest": "Estimated actual Forest 12 square miles."

L. Rudolph

Marsabit

Ituri Forest

Under

thirty

inches.

L. Kioga

Ruenzori

Mt Kenya

Over forty inches

Victoria

Nyanza

Kivu

L. Natron

Kilimanjaro

Meru

L. Eyassi

Pate

Hanang

Under

Usambara

L. Tanganyika.

Pemba

thirty

Zanzibar

inches

Nyuru

Uluguru.

L. Rukwa

R. Rufiji

Uzungwa

Mpagoro.

Rungwe

R. Ruvuma

L. Nyasa

| 0-3000 ft | 3000-6000 | over 6000 | forest | 40 ins. rain. | 30 ins. rain. |

MAP 1   East Africa: Mountains, Forests, Rainfall and Altitude.

and rises into mountains, such as the Usambaras and the Ulugurus, a rainfall of about 80 in. is precipitated[1], which appears to exceed anything definitely recorded elsewhere in East Africa except at the head of Lake Nyasa. The result is a magnificent forest formation at a comparatively low altitude. Apart from this, however, there is very little closed forest anywhere in East Africa below 3000 ft. and indeed by far the greater part is over 5000 ft. A large proportion of all the forest is confined to the lines of scarps looking towards the Indian Ocean. Their westward-dipping hinterlands lie in a rain-shadow where it is impossible for luxuriant vegetation to maintain itself under existing climatic conditions.

There is no doubt that the discontinuity of the forests so conspicuous on the map has been much exaggerated in recent historical times by human agency[2]. The agricultural development of the Uganda Protectorate has been at the expense of forest[3]. The Wa-kikuyu have wrought great destruction between Mount Kenya and the Aberdares. Europeans have swept away much forest west of Nairobi. The Wa-chagga have cleared the lower slopes of Kilimanjaro. The Pare Mountains have been almost completely deforested. The Wa-Bondei have cleared the eastern foothills of the Usambaras. The annual burnings by the Masai have continually eaten into the forest on the peaks along the southern end of the Rift Valley. The people on the coast have replaced the natural vegetation with cultivation.

All such operations as these have been so recent as to have no place at all on the evolutionary scale of time: we can be sure that at no earlier epoch was human agency so important. For the purposes of this enquiry the natural forest limits under present climatic conditions are correctly indicated only if we regard the map as modified to show:

(*a*) An appreciable amount of forest along the coast-line.

(*b*) A connection from Kilimanjaro to this strip, via the Pares and Usambaras, with no interruptions of greater width than 20 miles.

(*c*) A block covering most of the area Nairobi-Mt. Kenya-Aberdares.

(*d*) A more united forest west of the Rift Valley.

(*e*) Much more extensive forest between Ruwenzori and Victoria Nyanza.

THE GEOLOGICAL EVIDENCE.

Nilsson's conclusions were arrived at from a study of past glaciations on Mounts Kenya, Kilimanjaro and Elgon, and on the raised beaches of the Rift Valley lakes, Nakuru, Elmentaita and Naivasha. He found (*op. cit.* p. 255) that on Mount Kenya there were terminal moraines at about 4500 ft. ("huge"),

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[1] The average at Amani, on the seaward side of the East Usambaras, is 77 in.

[2] Some idea of the forest destruction in Kenya in recent times may be obtained by comparing Troup's map (1922) with Hutchins' (1909) and Johnston's (1902, Pl. VII).

[3] Cf. **Johnston**, *op. cit.* p. 66: "Except in the northern parts of Busoga the country is still thickly forested, and it was at one time one vast tropical forest like portions of Uganda [the original Kingdom, not the Protectorate], Toro and Unyoro."

3700 ft. ("two rather large and several smaller") and 3500 ft. ("small") below the existing glaciers. Between the arrangement of these glacial maxima and that of the maxima of Lake Nakuru a striking correspondence will be found.

Wayland's work is based on a variety of Uganda data[1]. He has come to the conclusion that East Africa witnessed two major pluvials, probably corresponding with the Günz-Mindel and the Riss-Würm Glacials of Europe, and a third wet phase, not of a magnitude justifying the appellation "pluvial," which may have corresponded to the Bühl Stadium. It will be observed that the agreement between these conclusions and those derivable from Nilsson's data is close. Wayland is satisfied that climatic changes, not land oscillation, were responsible for the phenomena from which the occurrence of the two pluvials has been inferred (1930, p. 472), and that the climatic changes were not merely local. It appears, indeed, that these two pluvials in East Africa were only the local manifestations of far more extensive climatic changes. After referring to the evidence that is to be found on every continent Coleman (1932) concludes that "There can be no doubt that at least two refrigerations in the Pleistocene affected the whole world contemporaneously."

Leakey has re-examined the Rift Valley lake-basins, Nakuru and Naivasha. He has been led to conclusions more detailed in some respects than those of the other workers, and they will be considered at length. Although Leakey's findings may not command universal acceptance in detail it is satisfactory to find that the sequence of the major events summarised below is in close agreement with that of the other authorities. The lake-levels all relate to Nakuru. The Naivasha evidence is not dealt with here as the hydrography of that basin is known to have been complicated by river capture. The dates, derived except for (vii) from Brooks (1922, p. 48, and *in litt.*)[2] are, of course, only to be taken as very general indications of relative remoteness. They are based on the contemporaneity, only assumed but of strong inherent probability and generally accepted, between the East African wet and the European cold maxima. Phrases in inverted commas are Leakey's.

(i) A long and severe wet period (Kamasian) coming to a close nearly 400,000 years ago.

(ii) A dry period accompanied by tectonic action[3].

(iii) A pluvial (Gamblian) during which the lake rose to 775 ft., declined to 250 and rose again to 510, finally coming to an end somewhere about 20,000 B.C.

(iv) A period during which the lake dried up completely. "The evidence

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[1] I have to thank him for separates and for a number of references.

[2] Since elaborated in Appendix B to **Leakey's** *Stone Age Cultures of Kenya Colony* (1931).

[3] Regarding this stage we know practically nothing, not even whether it was cold and dry or hot and dry: but as it will appear from subsequent discussion that its effects must have been largely overlaid by the subsequent pluvial, its importance for our present purpose is minimised.

for complete desiccation...is very strong...deposits of aeolian sand were formed."

(v) A wet phase (Makalian) marked by a rise to 375 ft. probably between 10,000 and 20,000 B.C.

(vi) A second complete disappearance of the lake. "We have further aeolian deposits at this period."

(vii) A minor wet phase (Nakuran) marked by a rise to 145 ft., the date of the climax being "estimated at 850 B.C."

(viii) At the present time Lake Nakuru is diminishing rapidly. In 1929 it nowhere exceeded 9 ft. 2 in. in depth, being 5 ft. 6 in. lower than when it was surveyed in 1906. Further, it may be calculated from the plan Leakey gives, that concurrently with this loss of depth the lake has shrunk from an area of about 21 square miles to 15·6 in the 23 years. (The former area is that delineated on the existing 1:250,000 map of the region, viz. G.S. 1764 Africa, Sheet South A-37/A dated March, 1918.) To some extent this reduction in the lake may be due to an accidental succession of dry years: but in view of the evidence for the retreat of the surviving glaciers on the peaks[1] it cannot be doubted that the shrinkage in the lake is due in part to a secular change.

The question arises of the extent to which the use of these lake-levels as criteria of pluvial intensity may be invalidated by tectonic movements. It is a fact that over a large part of the earth's surface the great differential crust movements, which had been set going in the early Tertiary, continued vigorously into the Pleistocene. East Africa in particular was the scene of tectonic activity on an immense scale. Three great shatter-belts manifested themselves, the effects of which are apparent to-day as three lines of eastward-looking scarps: (a) Usambara, Nguru, Uzungwa, with the secondary outlier Uluguru-Upogoro (Mahenge); (b) Aberdares, Mau, Mbulu, Hanang; (c) Ruwenzori, Kivu, Rungwe, West Nyasa. Under existing climatic conditions it is precisely on these scarps that evergreen forest maintains itself. Leakey expresses himself as satisfied that this tectonic activity was not responsible for the elevation of the Nakuru beaches for which he gives measurements, and that it may be considered as having practically come to an end before stage (iii). After stage (ii) the catchment area of Nakuru appears to have been uniform, and he believes that the physiography of the basin was not disturbed to any significant extent. It is to be noted, however, that stage (iii) is the period when Wayland concludes (1931, p. 44) that the hydrography of Uganda received its present shape. *Prima facie* this tends to invalidate the stage (iii) lake-levels as a criterion of the contemporary climate. But their status for this purpose is restored by the remarkable correspondence they exhibit with the second complex of Mount Kenya moraines. On the whole it is considered

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[1] Cf. **Savoyen** (1909, p. 449): "Im übrigen befinden sich sämtliche Gletschen des Ruwenzori gegenwärtig in starken Rückgang." And for Gregory's Glacier on Mount Kenya see **Nilsson** (1929, p. 255).

that we may accept Nakuru stages (iii) to (viii) with some confidence as indices of the climate prevailing over East Africa[1].

As regards the glacial evidence, it is, of course, a fact that the terminal moraine is formed at the point where the wastage of ice exceeds the supply. In other words it is determined partly by the temperature of the environment of the glacier and partly by the snowfall on the feeder slopes above. Therefore the altitude of a terminal moraine cannot be taken as a measure of either the precipitation or the temperature, only as an integrator of both. But these two climatic factors are precisely those that in combination determine forest growth. So that, above a minimum temperature, the extent of the glaciation is, very broadly, an indication of the extent of co-existing forest growth.

FORESTS AND CLIMATE.

As a basis for arriving at the climatic requirements of closed forest, which vary with the altitude, the existing forest types and their limits may briefly be described. Most of the information regarding the Kenya and Uganda forests is derived from Troup (1922). I am indebted to Mr R. M. Graham, of the Kenya Forest Department for particulars of the coastal forests.

These are arranged in descending order of rainfall requirements.

(a) Magnificent evergreen forest comprising a great variety of species and very rich in endemics and West African affinities. Found only on the Usambaras, Ngurus and Ulugurus[2] with a well-distributed rainfall of at least 70 in. and a climate that is neither tropical nor subject to frosts. These conditions are found in so narrow a belt on the east side only of the mountains, that the total area of this type of forest cannot exceed 300 square miles, in three blocks 80 miles apart.

(b) Tall semi-deciduous forest characterised by *Sterculia appendiculata* K. Schum., *Albizzia sassa* Macbride, *Trema guineensis* Ficalho and *Chlorophora excelsa* Benth. and Hk.f. It apparently requires between 50 and 60 in. of rain in an almost fully tropical climate and is at the present day practically restricted to vestiges on the Shimba Hills near Mombasa and on the eastern foothills of the same mountains as type (a) forest, into which association it merges at an altitude between 2000 ft. and 3000 ft.

(c) "Temperate Rainforest" of Troup, a tall evergreen community in which the dominants are *Ocotea usambarensis* Engl. ("Camphor") or *Podocarpus* spp. or both. "The minimum rainfall...is probably about 55 in. to 60 in." (Troup), and the climate temperate. Much of the Mount Kenya, Aberdares, Kilimanjaro and Usambara series forest is of this type. It still

[1] Mr A. Walter, Director of the British East Africa Meteorological Service, has pointed out to me that as the area has been one of volcanic activity the possibility of an accession of water from plutonic sources into the lake at some date or other cannot be entirely excluded.

[2] These three mountains will constantly be bracketed together in the following pages and for convenience I shall refer to them as the "Usambara series."

clings to Mounts Ufiume and Hanang, south-west of Kilimanjaro (Phillips, 1929, p. 363), and it furnishes the bulk of the evergreen forests of the highlands in the south-west corner of Tanganyika Territory. The lower limit in Kenya is now 7000 ft., but it descends to 5000 ft. elsewhere.

(*d*) Semi-deciduous coastal forests (*Brachylaena Hutchinsii* Hutch., *Afzelia quanzensis* Welw. and many other species) occur in patches close to sea-level with a fairly well-distributed rainfall of about 50 in. The Sokoke-Arabuko is the only considerable area.

(*e*) The Uganda evergreen forests are various, but it appears that some of the most. generally important trees are *Entandrophragma* sp., *Maesopsis eminii* Engl., *Podocarpus* spp., *Chrysophyllum* spp. Troup gives no indication of the rainfall, but from the isohyets given in the Meteorological maps of the Atlas of Egypt it appears that these forests subsist on about 50 in. at a general altitude not appreciably above 4000 ft.

(*f*) "Plateau Forests" of Troup (partly deciduous) found chiefly in the neighbourhood of Nairobi between 5000 and 6500 ft. Some typical trees are *Brachylaena Hutchinsii* Hutch., *Croton megalocarpus* Hutch., *Olea chrysophylla* Lam. Rainfall 40 in., climate equable and similar in temperature to that of type (*a*).

(*g*) "Cedar Forest" (*Juniperus procera* Hochst.) occupies a good deal of the Kenya Highlands. According to Troup its "true home is at an elevation of 7000–9000 ft. (i.e. well above the frost line) with a rainfall of 40–55 in. In the West Usambaras it is fully developed at 6000 ft., where it exists with a rainfall of under 40 in., not well distributed but supplemented by much mist.

It will be noticed that between the upper limit of type (*b*), Tall Semi-Deciduous Forest, at about 2500 ft., and the lower limit of types (*c*) and (*f*), the Temperate and Plateau Forests, which under natural conditions seems to be about 4500 ft., there is no forest in existence except that of type (*a*), which gets 70 in. of rain. There is no doubt that this is what may be described as an accidental result of the local physiography, for at the present time there is no part of the eastern half of our region between 2500 ft. and 4500 ft. that receives more than about 35 in. of rain except where the Usambara series of scarps face the ocean and precipitate no less than 70 in. But Mr Greenway informs me that if 50 in. fell anywhere between 2500 ft. and 4500 ft. the result would probably be a forest much resembling type (*b*).

From the foregoing it appears that under existing temperature conditions we can expect closed forest to cover any country above 5000 ft. that receives 40 in. of rain, and below that level 50 in.[1], provided that it is well distributed

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[1] For the present purpose soil factors are ignored, especially as the majority of the East African soils are evidently capable of supporting closed forest. One apparent exception is "Black Cotton Soil" (**Nicholson**, *op. cit.* p. 21). There the inability to support forest is probably to be regarded as the result of faulty drainage, for this type of soil is developed in situations that are waterlogged during part of the year.

and probably augmented to some extent by occult precipitation. As regards the estimation of the last element, Nicholson (*op. cit.* p. 16) quotes Phillips to the effect that it may amount to as much as 25 per cent. of the precipitation measured in the rain-gauge.

The importance of a proper distribution can hardly be overestimated. Chapin (1923, p. 111) remarks that in parts of the Upper Congo (which are below 3000 ft.) with a rainfall of 65 in. "a superb unbroken forest persists because there is seldom a month without rains," whereas in parts of Sierra Leone "where there is a dry season of four months, a total annual rainfall of 170 in. does not suffice for a continuous forest growth." As regards the degree of distribution necessary, it appears from Chipp (1927) that in the Gold Coast forest of a good type maintains itself within a thousand feet of sea-level with a rainfall of no more than 50 in. falling on 75 days, divided between every month in the year, and associated with a steady high relative humidity (over 80).

Now the total rainfall in a region of mountains or within the influence of a large body of water—and such is the greater part of East Africa—consists primarily of two elements, monsoon rainfall ("the Rains") and "instability rains." The latter reduce the desiccating effects of the periods between the Rains proper and are the element in the total rainfall that gives the effect of better distribution. Nicholson (*op. cit.*) has demonstrated the important effects of montane forest in inducing instability rainfall. We may take it then that when isolated forests begin to spread, under a favourable general change of climate, from the mountain-tops to which they have been reduced in a dry period, the distribution of the rainfall undergoes local improvement and the process of reafforestation tends to be accelerated by the beneficial influence they themselves have upon the local climate. In fact, even if a favourable change of climate does not of its own nature involve a better distribution of rainfall, its secondary effects do so. Further, as the areas of forest and the rainfall increase, there is a tendency for the temperature to fall, thus reducing evaporation. Therefore once a forest sheet had been established it should be able to maintain itself after the full extent of the beneficial secular change of climate originally responsible for the forest extension had begun to wane. Moreover, any general drop in temperature would have the effect of bringing to a lower level the montane forest associations, which have smaller rainfall requirements than the lowland types.

As may be seen from the map, much of the country in the interior of East Africa receives under 30 in. of rain; but none of it is appreciably below 4000 ft. in altitude. Therefore, a general increase of between 15 and 20 in. in the rainfall should suffice to cover it in time with forest. Much of the coastal strip already receives enough rain to support forest if human intervention is eliminated, and the same applies to the country north of Victoria Nyanza. Inland from the coastal strip until the highland area is reached the

rainfall in Tanganyika—e.g. between the Usambaras and the Ulugurus—is at present about 15 in. below the 50 in. required, as we have seen, to produce forest at such low altitudes, while in Kenya ("Taru Desert" and northwards) there is a deficiency of quite 25 in.

On the whole we may conclude that with a general increase of 15–20 in. in the rainfall throughout East Africa all the existing forest islands would be in communication with each other and with the Congo-West African forest. Under such conditions the low-level eastern part of Kenya would however probably still be clothed with no association more dense than Savannah. A slight general increase would of course have much more effect on forest distribution in some districts than in others. One of its first effects would be to connect the forests on both sides of the Rift Valley and to strengthen the connection across Uganda. In the next stage the Kilimanjaro-Usambara system would be brought into communication with the Kenya Highlands. But the junction of the northern and the southern mountain systems of Tanganyika Territory with the Ulugurus, and ultimately with each other, would hardly be effective until later still because of the low altitude of the country surrounding the Ulugurus.

THE PLUVIALS.

It is realised at the outset that any attempt to calculate rainfall in terms of inches from the fluctuations in the lake-levels breaks down. There are too many unknowns: for example we do not know the proportion of the total precipitation that gets into the lake or the relation that the evaporation bears to the volume of water in the lake; and both are constantly varying with the distribution of the rainfall, the vegetation of the catchment area, and the average depth of the lake. But nevertheless it is possible to draw certain conclusions for our purpose.

The Kamasian.

During this period the lower limit of the glaciers was on all the great peaks at least 4000 ft. lower than it is now. Moreover, as Nilsson deduces from the fact that the glaciers descended equally on all sides of the mountains, the precipitation must have been better distributed than at the present time. In sum, the general climate then was vastly more favourable to forest growth. If we accredit half of the 4000 ft. glacial advance to increased precipitation and half to lowered temperature we arrive at the conclusion that the climate must have been some 8° F. cooler (using the world-wide average factor of 3–4° F. per 1000 ft. altitude quoted by Willis (1922, p. 44)). In other words all the vegetation zones in East Africa were lowered 2000 ft. by the temperature factor alone, and montane forest capable of subsisting on 40 in. of rain could maintain itself down to within 3000 ft. of sea-level. But at the same time

precipitation was much greater and better distributed than now. The impression is irresistible that at this epoch the whole of East Africa was covered with a sea of forest in full connection with the West African.

So far as temperature was concerned the whole of the interior plateau of Tropical Africa must have been "temperate," in enjoyment of a climate no more exacting than that now prevalent at 5000 ft. in forested districts. These conditions are held to have continued for what was, even on the geological scale, a long period. The probabilities are surely strong that what in the Introduction I have called the "Temperate" fauna of the peaks to-day is representative of that dominant throughout Tropical Africa during the Kamasian.

The only islands in this sea of forest would have been those spots where the soil was unsuitable and those above the timber-line. With the lowered general temperature this line would have fallen correspondingly, by 2000 ft. or more, so that all the country above 7000 or 8000 ft. was bare of forest. Under these conditions most of the islands of Alpine vegetation would still have been separated, although some of them, e.g. on the Mau, the Aberdares and Mount Kenya, would have been in sight of each other.

The Gamblian.

With its glacial extension only 1000 ft. less in altitude than the Kamasian and still 3000 ft. below the present, the climate of the Gamblian was evidently almost as highly favourable to forest growth as the Kamasian. Doubtless the glacial extension was due in part to increased precipitation and in part to lowered temperature. The latter factor by itself would have made it possible for montane forest requiring only 40 in. of rainfall to grow down to 3500 ft. If the concurrent increased precipitation amounted to no more than 15 or 20 in. above the present it would have sufficed, as we have seen, to link all the present forest islands. The existence of a Lake Nakuru that was 65 times as deep as the present and held several hundred times as much water derived from much the same catchment, seems to assure us of this. It is not possible to base any arguments on the actual level attained by the lake because it is not clear whether it was in connection at its maximum with Lake Naivasha, and so provided with an outlet. On the whole, the Gamblian, too, is acceptable as an epoch of continuous forest: and the probability is that to this epoch the "subtropical" fauna of the mountains owes its dispersion.

The Makalian.

The Makalian is much more difficult to evaluate. It has been comparatively easy to come to the conclusion that both the Kamasian and the Gamblian pluvials were of first importance in contributing to the present distribution of living things in Africa. We shall find equally good reason for deciding that the last wet phase, the Nakuran, was of trifling significance. But the

Makalian falls between the Gamblian and the Nakuran, in intensity as well as in time.

The most superficial comparison would seem to indicate that in degree of favourability to forest growth the Makalian was nearer to the Nakuran phase than to the Gamblian. For the Makalian lake-maximum was 375 ft., compared with 145 in the Nakuran and 775 in the Gamblian, while the glacial extension was only a few hundred feet (350 ft. on Mt Kenya) below the present, against 3000 ft. below in the Gamblian. In other words, granted that there was an increased precipitation, the temperature could not have been appreciably lower than now, and any extension of forest growth depended on the precipitation factor alone.

Any attempt to estimate the Makalian rainfall must be based on the maximum attained by Lake Nakuru. A rise to 375 ft. looks imposing, but it cannot be accepted without analysis as evidence of a climate more favourable to forest growth to a significant degree. Unfortunately analysis involves large assumptions and the calculations can only be speculative.

We have three relevant facts of importance:

(*a*) With its surface 375 ft. higher than to-day it was in connection with Lake Elmenteita.

(*b*) The area of the combined lake was slightly over 200 square miles with a catchment of some 545, compared with an area of $15\frac{1}{2}$ in a catchment of 420 in 1929[1], i.e. 13 times as great, with a catchment 30 per cent. greater.

(*c*) The present Nakuru catchment rainfall is 37·5 in., so that the general addition of 15–20 in. that we have decided would be required for continuous forest growth, would bring the Nakuru figure to about 54 in. ($=4\frac{1}{2}$ ft.).

We do not know:

(*d*) The loss by evaporation (in inches per annum) referred to subsequently as E.

(*e*) The "run-off," i.e. proportion of total precipitation reaching the lake. This will be called P. In any attempt to work out the volume of water entering the lake it must be remembered that the wastage that is the complement of P does not occur with the rain that falls on the lake surface itself. In dealing with Nakuru this is a most important reservation, because at its Makalian maximum it occupied more than a third of the catchment[2].

Now probably the only figures we have of value for E and P in the case of an Equatorial lake are those arrived at by Hurst (1925) for Victoria Nyanza, viz. 1310 mm. ($=52$ in.) and 10 per cent. respectively. We do not know how the run-off conditions of Nakuru and Victoria differ, but applying the 10 per cent. to Nakuru as a trial we can calculate that on the existing rainfall and

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[1] These figures are worked out from the plan of the lake in Leakey's paper (*op. cit.*) and from G.S. map No. 1764, Africa 1:250,000 sheet South A–37/A dated March 1918.

[2] **Leakey** (1931, p. 505) notes that "during the excessively wet period from November 1928 to May 1929, when the Nakuru district got nearly treble its normal rainfall, the lake level rose only 24 in." Such definite figures aroused the hope that they might be utilised in this enquiry, but in seeking to ascertain what the "normal rainfall" for the months cited might be, I failed to find the "excessively wet period" reflected in the records at my disposal at Amani. I therefore applied to Mr A. Walter, Director of the British East African Meteorological Service, who has kindly furnished me with the figures actually recorded for each of the 7 months in question at five stations in the Nakuru catchment. They are all below the average, not 200 per cent. above. In any case, as Mr Walter points out, a lag, perhaps very considerable, is to be anticipated between abnormal downpour and lake-rise. This lag is not of course significant when we are dealing with a secular change.

lake-area E would be 130 in. a year or over 0·3 in. a day. This is about 0·1 in. less than the average rate of evaporation at Aswan[1], where the saturation deficit is certainly much greater than it is at Nakuru. This indicates that 130 in. is not too low a figure for E at Nakuru under existing conditions, but is on the contrary probably rather high. $E = 100$ in. might be nearer the truth and it can be calculated that this would connote $P = 6·6$ per cent. But under the conditions of the Makalian maximum the present difference between Nakuru and Victoria in the matter of loss by evaporation could hardly persist. For, broadly, a higher rainfall is associated with a higher relative humidity, and Nakuru being at a higher altitude than Victoria, the mean temperature would be lower. Both these factors would tend to lower the saturation deficit of the Nakuru district relatively to Victoria. At the Makalian maximum, then, E for Nakuru would, by inference, have been less than the present 100 in., and may well have been as low as for Victoria now (52 in.). With the increasing size of the lake the exact value of P becomes less important for our calculation, since ultimately the rain that fell on the 200 square miles of lake-surface provided seven-eighths of all that reached the lake. If we work out the rainfall that would have been necessary to maintain the Makalian lake at its maximum (a) with $E = 100$ in. and (b) with $E = 52$ in., we get for (a) 85 in. and (b) 44 in. But a saturation-deficit so high as to cause a loss of 100 in. by evaporation could hardly exist with a rainfall of 85 in., so that the truth must lie nearer the 44 in. rainfall.

We may attack the problem from another side. Given a rainfall of 54 in., which is, we have decided, about the minimum conducive to a general afforestation, what value does that connote for E? For our purpose the level at any stage may be taken as constant: for although it was actually rising, several thousand years are available for the total rise of 375 ft. and the average annual change would have been only an inch or two. With the same rainfall E varies with the size of the lake. Thus with a 55 in. rainfall and the lake-area approximately 50, 100 and 200 square miles, we get evaporation figures of 80 in., 70 in. and 60 in. respectively. But it is obvious that with a rainfall of 55 in., actually higher than that of the Victoria Nyanza basin now, and a saturation deficit that should certainly have been no higher, the loss by evaporation ought to be less, not more. On these grounds therefore it seems improbable that the Rift Valley rainfall during the Makalian reached 55 in., though it may have been 12 in. or so above the present.

Speculative as all these arguments admittedly are, they point in the same direction. They all give us cause to doubt whether the Makalian rainfall was sufficiently greater than the present to permit of general forest growth. Some of the forest islands would have been linked, all those in the Kenya Highlands with each other and probably with Ruwenzori and the Kilimanjaro-Usambara Chain: but with temperatures much as they are to-day, the montane forms, "subtropical" as well as "temperate," would have remained restricted to their mountains.

The Nakuran wet phase.

A lake 145 ft. deeper than Nakuru to-day bulks large, and seems to demand a considerably increased rainfall. But between the end of the Makalian wet phase and the maximum of the Nakuran at least 10,000 years elapsed, so that 4000 may reasonably be allocated for the lake to fill up for this last wet phase. The average rate of rise would then have been about $\frac{1}{2}$ in. a year, instead of the present drop of $2\frac{1}{4}$ in. From the contours it appears that the lake at the Nakuran maximum would only have had about twice its 1906 area of 20 sq.

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[1] Quoted by **Kirkpatrick** (*The Mosquitoes of Egypt*, Cairo, 1925) from *Climatological Normals for Egypt and the Sudan etc.* issued by the Physical Department, Ministry of Public Works, Egypt, 1922.

miles. How much more rain than the present annual fall would suffice to turn a deficit of $2\frac{1}{2}$ in. into a gain of $\frac{1}{2}$ in. for a lake of 40 sq. miles? The answer, using the figure of 6·6 per cent. for P that we reached in the preceding section, is barely 2 in. Doubtless the lake varied in its rate of rise and often gained more than $\frac{1}{2}$ in. in a year. But the more rapid the gain the shorter the period during which the high rate of gain can have continued. In any case, it can be calculated that even a 6 in. rise in the lake could have been accomplished on a rainfall $5\frac{1}{2}$ in. above the present. The inference is that the Nakuran wet phase had no important influence in extending forest growth.

<div align="center">THE DRY PERIODS.</div>

The first, post-Kamasian, dry period is quite incalculable in extent, but the next two dry periods are susceptible of some examination. At first sight the establishment of two epochs when Lake Nakuru dried up[1] would seem to indicate periods of drought severe enough to exercise a catastrophic effect on forest growth throughout East Africa. A recent reviewer of Leakey's *The Stone Age Cultures of Kenya Colony* (*Nature*, No. 3242, p. 1021), who refers to the "intensely desertic conditions" of the post-Gamblian inter-pluvial, would doubtless accept this view. Important considerations exist, however, to modify our conception of the severity of the inter-pluvials' effect on the forests.

(*a*) Although Lake Nakuru still bulks large upon the map it is, compared with its former size and depth, a mere vestige, still diminishing. During the last, and least, of the wet periods we have been considering it was over 150 ft. deep against 9 ft. 2 in. in 1929. In fact in the 23 years following 1906 it lost 5 ft. 6 in. As has been pointed out above, the deficiency in rainfall is due, in part at least, to a secular deterioration in climate. If it continues, even without intensification and with the maintenance of the existing rainfall of 37 in. a year in the catchment, Lake Nakuru will have dried up completely before the end of the present century.

(*b*) The deposits of blown alluvium in the bed of the lakes following the Gamblian and Makalian wet periods do not of necessity imply a climate much drier than the present one[2]. I am informed by eye-witnesses that in the section of the Rift Valley concerned there is already a considerable transport of soil by wind, to such an extent indeed that on one local sisal estate the soil has been compacted with heavy rollers to reduce the loss by wind-erosion.

[1] **Leakey** (*op. cit.* p. 501) refers to "complete desiccation" but it is not clear whether it has been established that the desiccation extended to the area covered by the present lake, which must presumably always have been the deepest part of the basin.

[2] Dr K. S. Sandford has pointed out to me that dust blows readily from any exposed alluvium. It forms banks of "aeolian material," which when old looks like loess and may come to be called by that name. He has recalled particularly the example of the mudbanks temporarily exposed at low Nile. The dust clouds they gave rise to as soon as the water had left them were a familiar phenomenon to us both. Thus a seasonal exposure for a few weeks every year may be capable of ultimately producing a loess-like formation in the neighbourhood.

(c) In the Introduction attention was drawn to the fact that the Usambara series are distinguished among East African mountains by the strength of their West African affinities, both zoological and botanical. Moreover the Usambara Series are inhabited by a surprisingly large number of distinct species, known from no localities outside these extremely restricted mountain forests. Examples are *Malaconotus alius* Friedm., *Apalis moreaui* Scl., *Ploceus nicolli* Scl., *Artisornis metopias* (Rchw.) among birds: *Pterocarpus Zimmermanii* Harms, *Cephalosphaera usambarensis* Warb., *Berlinia Scheffleri* Harms, *Sloetiopsis usambarensis* Engl., among trees.

The greatest abundance of vestigial forms, both endemic and West African, survive precisely in those spots that are unique in East Africa by reason of their copious rainfall—amounting to between 60 and 80 in. very well distributed—in a zone that is neither fully tropical nor subject to frost: and it is a legitimate inference that the forms in question are unable to survive under any more rigorous conditions. Now they are at the present day extremely restricted; any pronounced general deterioration in climate would result in the complete disappearance from East Africa of the delicately balanced conditions in which they live, and they would vanish too. Their survival till the present day tends to show that the inter-pluvials we are discussing cannot have involved very severe general desiccation.

(d) A general drop in rainfall sufficient to have a marked effect on the Rift Valley, which with 37 in. already shows a tendency to dry up, would not necessarily much affect the total area of the forest elsewhere. The Nakuru district would indeed be "intensely desertic" if the average rainfall fell another 10 in., but the greater part of the existing forests have as wide a margin of safety as that. Within their limits there would, of course, be some readjustment of the zones of the several types, "temperate rain-forest" for example tending to be replaced by "plateau forest" or "cedar"; but only that fringe of the forest area already maintaining itself on a minimum rainfall would be lost. If the 27 per cent. drop in rainfall which 10 in. in the Rift Valley represents were general, the effects would be more serious. Most of the existing "cedar" areas would disappear, and that association would largely replace "temperate" forest where it now occurs. Uganda, the chief corridor to the West African forests would be extensively denuded. But in comparing former dry periods with that in which we live it must constantly be remembered that the East African forests have suffered more diminution through recent human agency than they would have through an appreciable drop in rainfall.

All these considerations tend to show that the climates of the two interpluvials had not necessarily a catastrophic effect on forest growth. They may even not have been much more severe than that of the present day. This conclusion, in so far as it depends on consideration (c) applies with especial force to the post-Makalian dry period: for if the specialised forest life of the

Usambara series had been swept away in the post-Gamblian, it is just possible that the Makalian pluvial may have been long enough, and sufficiently important in extending the forest, to enable even mountains within sight of the Indian Ocean to be restocked with West African forms. But if these types had been swept away in the post-Makalian the Nakuran wet phase could have done nothing to repair the loss.

SUMMARY OF CONCLUSIONS.

I desire to emphasise that in a summary of this nature the statements made must inevitably appear to be more definite and precise that I should wish or than the present evidence warrants. In particular the dates are to be understood as nothing more than indications of relative remoteness from the present. "Forest" is to be read as "Evergreen Forest."

Present forest boundaries are generally not natural. They have been reduced by human agency as much as they would have been by an appreciable drop in rainfall.

A general increase of from 15 to 20 in. in the rainfall of East Africa would be sufficient to cover practically the whole of it in time with forest.

Communication of the existing forest islands with each other and with the West African forest existed under Temperate climatic conditions for a long period prior to 400,000 years ago. To this epoch (Kamasian) is ascribed the dispersal of the species now confined to the upper part of the montane forests. Evidence that the existing Alpine areas were in direct communication during the Kamasian is, however, lacking.

After an interval of which we know nothing, Kamasian conditions were re-established in a somewhat modified form and continued until about 22,000 years ago. So recently, then, as this latter date montane forest forms—probably those now typical of the lower zones—were dominant throughout the East African interior, and West African influence could penetrate to within sight of the Indian Ocean. The subsequent dry period may have been severe enough to obliterate forests in some areas where they exist to-day, but wholesale destruction probably did not take place.

Before 12,000 years ago the forest sheet was in part re-established, but under temperature conditions similar to the present; so that montane forms were generally restricted, as now, to high ground. For these it is possible that communication was open from Elgon to Kilimanjaro and the Usambaras. But it is unlikely that the highland forms in Southern Tanganyika Territory were in communication with the Northern, or the Ulugurus with either.

The subsequent dry period may have been hardly more rigorous than that now being experienced. The wet phase that reached its maximum 2800 years ago was, beyond question, insignificant.

It follows that up till 22,000 years ago opportunities continually occurred for the flora and fauna of montanes now isolated to be assimilated with each

other and with West Africa. It is only for certain during the last 12,000 years that the conditions of isolation favourable to race differentiation have been fully developed.

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THE RIVER AS A FACTOR OF PLANT DISTRIBUTION

By S. ILLICHEVSKY.

In the spring of every year the rivers that flow through the plains of Eastern Europe and of Siberia begin to overflow and inundate their valleys. The snow accumulated during the continuous cold winter, especially in the northern forest regions, which gather immense quantities, rapidly melts with the great spring rise of temperature. The current of most of the rivers is slow on account of the flatness of the land, and the thaw thus causes very extensive flooding. Thus the Dnieper at Kiev in the spring of 1931 rose 8·52 m. above its ordinary level, and its tributary, the Desna, about 8 m. As the territory drained by these rivers is comparatively flat it is natural that the spring floods should cover immense areas, inundating forests, fields and villages, so that one may often see a lake 10 km. broad spreading over the river valley to the horizon. This lasts for a month or six weeks, and then the river gradually retreats between its proper banks.

During the flood a thick layer of comparatively cold water covers every-thing, and plants growing in the inundated area must suffer a check in growth, being deprived of air and warmth and partly of sunlight. Many plants perish under such conditions, while others live on through the summer without any visible damage. Thus the vegetation of that portion of the river valley which is inundated—the greater part of it every spring—must differ more or less sharply from the vegetation of upland (non-inundated) parts of the valley. No matter whether the river is great or small it inevitably floods its valley in the spring.

The common structure of the river valleys in Eastern Europe, as worked out by Prof. G. Tanfiliev about forty years ago, is as follows. On the right bank of the river we have an upland plateau with argillaceous soil (loess), chernozem, or chalky soil (generally rich in calcium carbonates); then we come to the alluvial (inundated) part of the valley with the river itself. On the left bank of the river is a belt of alder swamps; then the slope of the so-called "second (sandy) terrace of the left bank" and the terrace itself (a sandy plateau), and finally—sometimes after a belt of peat or saline bogs occupying the inner part of the sandy terrace—we come to the gradual slope of another plateau (the third terrace, chiefly chernozem). It is generally supposed that a river formed its valley by changing its course in the valley area, and that it could never fill the valley channel ("Talweg") completely; but if we consider the modern floods which cover the whole valley up to the second sandy terrace, we may well suppose that similar, and probably much greater floods, were habitual during the Ice Age when colossal masses of frozen water, incomparably greater than the modern snow layer of the winter

in the temperate zone, must have thawed gradually during the summer, as the winter snow thaws now in the spring. Then the normal summer bed of a river would occupy the whole bottom of the river valley, so that the "second terrace" may well be the true bank of the giant river of the glacial period. And it is not impossible, I think, that in an exceptionally hot summer even this second terrace would have been covered with water, especially during the period of the glacial retreat. Modern rivers do not fill the bottoms of their valley except in a few cases, and then chiefly in the middle parts of their courses. It is in these middle parts that there exists a zone which is flooded every year, and it is natural that this zone should differ considerably in its vegetation from other non-inundated parts of the river valley and plateau.

We may now ask—in what do the differences consist? My botanical investigations during many years, in several parts of the Northern Ukraine in the basin of the Dnieper, have provided plenty of material for answering this question, and it has been possible to compile a list of plants which avoid, and a corresponding list of those which inhabit, the inundated areas. The investigations were made in the river valleys of the left bank tributaries of the Dnieper, namely the Desna (at Chernigov and partly at Novgorod-Seversk), the Soola at Loobni and its tributary the Oodai in a number of places, the Vorscla at Poltava and at two places respectively 45 and 60 km. to the north, and the Orel with its tributaries (three separate localities). At Poltava especially I made precise and systematic observations over a long period (about 14 years), so that it is possible to state with almost perfect accuracy the connection between many plants of the Poltavan flora and the inundated areas. Calculations of the numbers of species growing in various belts of the river valley at Poltava have given some very interesting results, showing the great differences between the systematic composition of the several belts. The chernozem belt at Poltava was not so carefully investigated, and the figures for this belt are therefore omitted. The numbers and percentages of species growing in three of the belts are as follows:

	Right bank (clay)		Left bank Inundated belt		Left bank 2nd sandy terrace		
	No. of spp.	%	No. of spp.	%	No. of spp.	%	Total
Total Angiosperms	586	61	379	39·5	363	38	960
Dicotyledons	497	66	283	36	282	36	754
Alsineae	14	67	7	33	15	71	21
Sileneae	20	80	11	44	11	44	25
Ranunculaceae	19	57	14	22	16	48	33
Labiatae	35	74·5	12	25·5	16	34	47
Monocotyledons	97	47	106	51·5	81	39	206
Gramineae	51	61·5	45	54	30	36	83
Cyperaceae	14	37	19	50	23	60·5	38
Liliaceae	15	54	7	25	12	43	28

Many species occur in several belts and therefore the total number of species is less than the sum for all the belts together. Some ecological charac-

teristics of certain families are seen very distinctly in this table. For instance, the monocotyledons are evidently more attached to the moist conditions of the inundated part of the river valley than the dicotyledons (51 per cent. of the whole number of monocotyledon species and only 36 per cent. of the dicotyledons), the Gramineae are more numerous (61 per cent.) in the rich soils of the belt on the right bank of the river, while the Cyperaceae prefer sand (60·5 per cent.), and the Liliaceae evidently avoid the moist inundated belt. The Alsineae prevail on the sandy soil belt (71 per cent.) while the Sileneae grow mostly on the rich soils of the clayey belt. The Labiatae are ecologically similar to the Liliaceae, avoiding the river belt and evidently prefer the argillaceous belt. Thus every belt has its own special characteristics. The specific composition of a belt community hardly changes, even for distances of hundreds of kilometres along the belt, while in passing across a belt the vegetation changes very distinctly, often in the space of a few hundred metres. For instance, the forests on the upper part of a river's course and near its mouth are almost identical, but the forests of the several belts at the same point are quite distinct in their composition and characters. A forest of the right (argillaceous) side of the river valley has at Poltava about 75 typical forest species, of which only 25 species (= 33 per cent.) grow also in the forests of the inundated belts and only 10 species (13 per cent.) occur in the dry forests of the second sandy terrace. The differences are therefore striking, and I think it would be desirable always to note on herbarium sheets, as well as in botanical accounts, not only the soil on which the plants grow, the frequency and other ecological details, but also the river valley belt (at any rate if the plants are from the inundated or non-inundated part), marking each by a distinguishing letter.

The specific calculations give other interesting ecological results: for instance the dry forests of the sandy belt have 43 species (about 30 per cent. of the whole number of species) in common with the virgin chernozem steppe, and 51 species (= 34 per cent.) growing also in dry meadows of the argillaceous (right bank) belt. But there is not a single steppe species in the forests of the argillaceous (right bank) belt. Thus a forest of the sandy belt and a forest of the right bank argillaceous belt are of quite different characters.

The distribution of the vegetation of these belts on the river valley terraces is another interesting point: the upland (right side) plateau with grey forest soil, the loess slopes of this plateau and the non-inundated parts of the river valley—the lowland—are almost identical in their vegetation and belong to the same belt. Even the slopes of the second (sandy) terrace are covered by the same vegetation. The sandy plateau of the second terrace as well as the inundated parts of the lowland[1] have a distinct vegetation. Thus these belts do not coincide with river terraces, nor with soil distribution, the same vegetation being found on grey forest soil, on sand, and on loess soils, while the

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[1] Which have also a sandy soil.

sandy soil of the inundated river valley and of the second terrace and of its slopes have all three quite distinct vegetations. It is evident that water is the chief factor determining the belt distribution.

I give here the lists of plants growing on one belt and of those avoiding it, taking for the sake of simplicity only the two chief belts: the flooded belt (R) and the non-flooded (upland, U); these lists contain only the species which in the whole of the investigated territory, i.e. in the basins of the above-named rivers, are always connected with one of these belts and never occur in the other, i.e. plants peculiar to each belt. Of the many species peculiar to each belt those which have a wide distribution, or which occur also in Western Europe and are therefore best known to the West European reader, were mainly chosen.

I. *Plants of the inundated belt which avoid the upland plateau belt.*

Potamogeton natans (and other spp.)
Allium acutangulum Schrad.
Fritillaria Meleagris L.
Orchis laxiflora Lam.
Salix purpurea L.
Nasturtium amphibium R.Br.
Sium latifolium L.
Ostericum palustre Bess.
Teucrium Scordium L.
Lycopus exaltatus L.
Veronica longifolia L.
Pedicularis lacta Stev.
Petasites tomentosus DC.

and many other species, such as *Koeleria Delavignei* Czern., etc.

II. *Plants of the non-inundated belt which never occur in the flooded region.*

Bromus erectus Huds.
Koeleria glauca DC. (only on second sandy terrace)
Stipa capillata L. (and other spp.)
Glyceria plicata Fr.*
Carex supina Whlnb.
C. Micheli Host.
C. pilosa Scop.†
Juncus glaucus Ehrh.‡
Allium rotundum L.†
A. sphaerocephalum L.†
Gagea lutea Schult.†
Stellaria Holostea L.†
Silene nutans L.†
Delphinium consolida L.
Anemone silvestris L.
Pulsatilla patens Mill (not in right bank belt)
P. nigricans Stoerk.
Corydalis solida Sm.
Sisymbrium Alliaria Scop.
Turritis glabra L.
Draba verna L.
D. nemorosa L.
Cytisus austriacus L.
Melilotus officinalis§
Trifolium alpestre L.
Viola hirta L.
V. odorata L.†
Viola mirabilis L.†
V. Riviniana Rchb.†
Peucedanum alsaticum L.
Seseli annuum L.
Pulmonaria officinalis L.
P. angustifolia L.
Ajuga genevensis L.
Salvia pratensis L. (right bank belt)
Thymus marschallianus Willd.
T. chamaedrys Fr.
Verbascum Lychnitis L.
V. phoeniceum L.
Veronica spicata L.
V. Teucrium L.
Pedicularis comosa L.
Asperula cynanchica L.
A. odorata L. (only right bank belt)
A. glauca Bess.
Campanula sibirica L. (not on sands)
C. persicaefolia L.
Chrysanthemum corymbosum L.
Senecio Jacobaea L.
Centaurea Scabiosa L.†
Tragopogon major Jacq. (not in the sand belt)
Lapsana communis L.
Taraxacum serotinum W.K.

and many other species.

* A marsh plant growing along the brooks, but never in the river belt; *Glyceria fluitans*, on the contrary, grows only in the river belt and not on the upland marshes.

† Not on second (sandy) terrace.

‡ A marsh plant, like *Glyceria plicata*, common along upland brooks but not found in the river belt, where other species of *Juncus* replace it.

§ Replaced by *M. albus* Desr. in the inundated belt.

Exceptions may be possible in other climates and other regions where a species of this (non-inundated) belt may be found on another (inundated) belt, and vice versa, but in the territory described I have never seen such exceptions.

The last conclusion from my investigations is that plant communities may be distributed in series, where several communities contain certain species replacing one another (e.g. certain Veronicas, Ranunculi, etc.) or vicarious species[1]. If my results are compared with those of other authors in literature dealing with more northern or more southern localities, it will be seen that a field or a meadow plant of the North may become a forest plant, or even a plant of alder swamps in my district. Therefore a species may change its habitat in a different latitude or a different climate and is evidently less plastic in relation to various ecological conditions than is generally supposed. In the same way palms and other tropical plants grow in greenhouses in temperate climates although they could not grow in temperate forests; and southern steppe or desert plants grow on warm southern slopes in temperate climates, while species of northern origin, which in their original climate are found in meadows, occur in shady forests or cold alder swamps in more southerly latitudes. Under such conditions even whole plant communities of a more northern and of a more southern type are to be found in juxtaposition; thus we have at Poltava, and other places in the neighbourhood, not only forest, steppe and meadow communities typical for this locality, but even a semi-desert or desert type of vegetation (on the dry sandy soil of the second terrace) with its scattered tussocks of grasses and spring ephemerals between them.

SUMMARY.

The vegetation in river valleys of the eastern part of the Eurasian continent displays a great and constant difference between the inundated and non-inundated parts of the valley. There are many species growing only in the parts of the valleys inundated in spring or, on the other hand, only in the non-inundated parts; thus we have two primary zones or belts quite distinct in their vegetation and not coinciding with river terraces nor with soil belts. In the same manner the vegetation of the "second sandy terrace" of the left bank is also quite distinct. And there are parallel species replacing one another in the several belts and zones just as there are in the several plant associations—"ecological series" of species. In different latitudes and climates plants change their habitats, and this change compensates for the lack of physiological adaptability, which is not so great as is generally supposed. In the same locality species and communities of more northern or more southern type exist side by side, ranging from desert vegetation to that of the northern swamps or tundra, each with its characteristic species, microclimate, soil conditions and even landscape.

[1] Better to call them corresponding species, as vicarious is a geographical, not a topographical term.

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And other papers by the author.

ON INTERMITTENT GERMINATION AS ILLUSTRATED BY *HELIANTHEMUM GUTTATUM* MILLER

BY MISS D. V. JUBY, B.Sc.

AND

MISS J. H. PHEASANT, B.Sc.

(With one Figure in the Text and one Folding Graph.)

HELIANTHEMUM BREWERI Planchon exhibits markedly intermittent germination, to the biological importance of which attention has been drawn (cf. Salisbury, *Biological Equipment of Species in Relation to Competition*, This JOURN. **17**, p. 219), Prof. Salisbury therefore suggested to us the desirability of investigating the germination of a similar type, namely *H. guttatum*, with a view to elucidating the degree of constancy of this feature and the causal factors involved. These investigations were carried out in the Botanical Department, University College, London.

Ripe capsules of *Helianthemum guttatum* were collected between August and October 1930. The seeds therefrom were used in our germination tests. Shallow, round glazed dishes were used as germination pans. Finely sifted loam was placed in each dish to a depth of about ¾ in. The soil was then pressed down evenly but lightly, well moistened with tap water and covered with a thin layer of sand previously sterilised by boiling with water. Any foreign seeds present in the soil which germinate, can therefore be detected and removed, as they have to penetrate the sand layer. In general, 100 seeds were sown in each pan on top of the sand, and the pan was covered with a sheet of glass. Thus the layer of air inside the pan above the level of the seeds was more or less saturated with water vapour, and conditions were comparable with those obtaining inside a Wardian case. The sand was kept moistened daily with tap water, and the seedlings removed after the appearance of the plumule. This procedure eliminated error due to possible "pseudo-germination." The date of emergence of the radicle was taken as the day of commencement of germination.

In all, 25 sets of 100 seeds each were sown in this way. The results obtained were detailed in germination graphs. The number of seeds germinating in one day were presented as ordinates, and the number of days after sowing, when germination occurred, as abscissae. The collective graph for the entire 2500 seeds is shown in Fig. 1. The results are set out in the accompanying table.
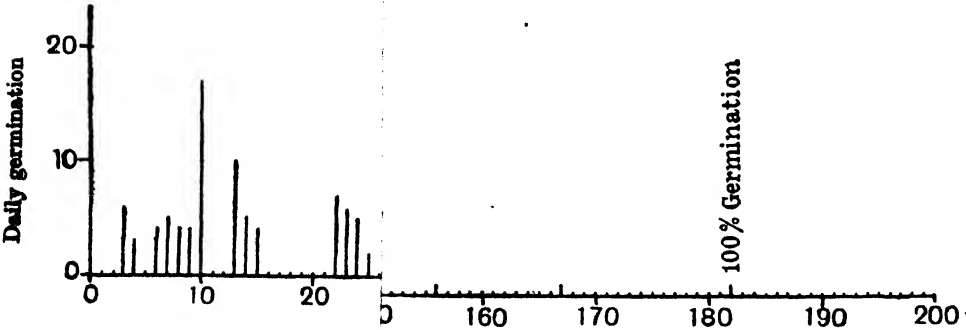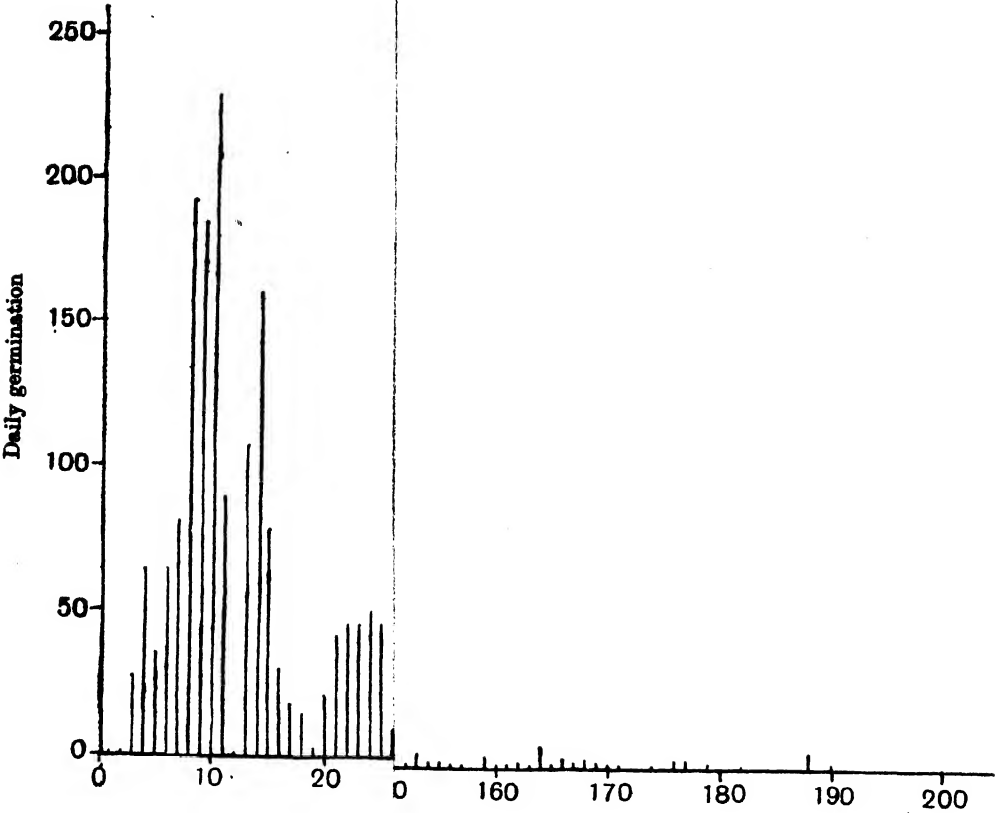
n of 100 seeds.

No. of days after sowing 1–2 mm.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
3	–	1	–	–	–	–	1	4	6	8	2	–	–	–	–	–	–	–	–	–	2	–	3	–	–
4	1	1	–	2	–	1	4	1	3	3	2	2	1	1	–	1	3	3	11	5	2	6	5	1	5
5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	8	3	5	10	9
6	1	2	4	–	–	4	9	5	4	4	2	6	–	–	–	–	–	5	13	5	–	–	–	–	–
7	–	2	4	–	7	2	4	3	5	2	2	2	9	2	4	3	6	7	2	5	–	–	5	5	–
8	6	6	10	4	–	5	2	5	4	4	8	5	16	19	18	24	15	3	1	5	5	7	3	10	7
9	5	9	1	6	13	11	3	18	4	18	9	3	2	7	7	8	9	3	6	7	10	6	6	–	13
10	19	8	19	18	8	6	6	11	17	12	8	17	4	–	6	2	5	7	4	5	16	3	16	10	2
11	4	2	3	4	5	4	–	–	–	–	–	–	12	2	12	16	8	1	–	3	–	2	4	6	–
12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13	6	7	1	3	3	6	12	15	10	9	10	22	–	–	–	–	–	–	–	3	–	–	–	–	–
14	2	5	8	2	–	2	13	2	5	4	12	9	21	26	12	14	19	1	–	1	–	1	–	–	1
15	1	4	2	3	–	1	13	1	4	6	6	3	2	4	5	2	3	5	–	4	–	1	–	4	4
16	1	1	–	1	–	–	1	–	–	–	1	–	6	3	2	2	1	1	1	1	3	–	–	1	4
17	–	–	–	–	–	–	–	2	–	1	1	–	1	2	3	3	1	–	1	1	–	–	–	1	–
18	1	–	1	2	1	3	–	–	–	–	–	–	–	–	–	1	1	–	–	–	4	–	–	–	–
19	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–
20	1	–	2	1	–	2	5	–	–	–	2	2	–	–	–	–	–	2	3	–	–	–	–	–	–
21	4	4	3	4	5	–	4	2	–	–	–	5	–	–	–	–	–	2	4	3	–	–	–	–	1
22	–	1	1	–	2	3	1	8	7	3	4	10	–	–	–	–	–	–	2	2	2	–	2	–	–
23	1	4	4	2	2	1	2	4	6	6	8	2	–	–	–	–	–	1	–	1	–	–	–	–	1
24	3	3	3	–	2	1	–	2	5	2	1	–	7	5	3	4	3	–	–	1	1	–	–	3	1
25	2	–	3	8	3	–	4	3	2	6	4	3	–	–	–	–	–	5	1	1	–	–	–	–	–
26	–	–	–	–	–	–	3	–	–	1	4	1	–	–	–	–	–	–	–	–	–	–	–	–	–
27	1	2	2	1	4	–	–	–	–	–	–	–	–	–	–	–	–	3	4	3	–	–	–	–	–
28	3	2	–	2	–	2	–	–	–	–	–	–	–	–	–	–	–	3	1	–	3	1	–	–	2
29	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–	1	2	–	–	1	2
30	3	–	2	2	3	2	1	1	1	1	1	–	–	1	–	–	–	4	–	3	3	1	1	1	–
31	1	–	–	–	1	–	1	1	–	1	1	–	1	1	–	–	–	–	1	–	–	1	–	–	–
32	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	1	1	–	1	–
33	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	2	2	–
34	1	1	–	–	2	1	1	1	1	–	–	–	–	–	–	–	–	–	3	3	–	–	–	–	–
35	1	3	2	3	2	–	–	–	–	1	1	2	–	–	–	–	–	2	3	1	–	1	–	–	2
36	–	–	–	–	–	1	–	2	4	2	–	–	–	–	–	–	–	1	–	–	–	–	3	–	–
37	1	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	2	–	4	–	2	–	–	2
38	2	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
39	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
40	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
41	1	2	2	–	3	–	–	–	–	–	–	–	–	–	4	5	–	–	–	–	1	–	1	1	1
42	–	–	2	–	2	1	–	–	–	–	–	–	1	2	1	1	4	–	–	2	1	–	–	–	–
43	–	1	2	–	1	–	–	–	–	–	–	–	1	2	–	2	–	1	–	–	1	–	–	–	–
44	–	–	1	1	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	1	–
45	–	1	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
46	–	–	–	4	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
47	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
48	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	3	1	1	1
49	–	–	2	1	–	1	–	–	–	–	–	–	1	–	1	–	1	–	1	–	–	–	–	–	1
50	1	2	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–
51	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
52	1	2	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
53	1	1	1	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
54	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1
55	–	–	–	2	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	1
56	–	–	1	1	–	–	–	–	–	–	–	–	1	2	–	1	–	–	–	–	–	–	–	–	–
57	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
58	1	1	1	2	1	1	–	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–
59	2	–	1	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–
60	–	–	–	–	3	–	–	–	–	–	–	–	4	2	–	–	4	–	–	–	–	–	–	–	–
61	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
62	–	2	–	1	–	1	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
63	1	2	1	–	–	1	–	1	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	2	1
64	–	–	–	1	1	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–
65	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
66	–	1	1	2	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–
67	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	1	–	3	–	1	1	–
68	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
69	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
70	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	–	–	1	1	–	–	–	1	–
71	1	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	2	–	1	–	–
72	–	–	2	1	–	–	–	–	–	–	–	–	–	1	–	–	2	–	–	–	1	–	1	1	–
73	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

No. of days after sowing 1–2mm.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
74	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	1
75	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	2
76	–	–	–	1	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	3	–	–	–	1	1
77	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
78	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	1	–	–	–	–	–	–
79	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–
80	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
81	2	–	–	1	–	–	–	–	–	–	–	–	1	–	2	–	–	–	1	–	–	–	–	1	1
82	–	–	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
83	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
84	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
85	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
86	–	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
87	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
88	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
89	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
90	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–
91	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
92	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
93	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	4	–	–	–	–
94	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	1
95	–	–	–	–	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
96	–	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	1
97	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
98	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	–	–	–	–	–	–
99	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	2	1	–	–	–	–	–	–
100	–	1	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	1	–	–	–	–	2	1
101	–	1	1	1	1	1	–	–	–	–	–	–	1	–	–	–	–	1	1	–	–	–	–	1	–
102	–	–	–	–	–	–	1	–	–	–	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–
103	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–
104	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	–	1	–	–	–	–	–	–	–
105	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	1	–	–
106	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1	1	–	–
107	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
108	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–
109	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
110	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
111	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–
112	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–
113	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
114	–	–	–	–	–	2	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
115	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
116	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	2	
117	3	1	1	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
118	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
119	–	–	–	–	–	–	2	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	1	–
120	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
121	–	1	–	–	2	1	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
122	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
123	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
124	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
125	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
126	–	–	1	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	2	1	1	–	1	
127	–	–	1	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–
128	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–
129	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
130	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
131	2	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
132	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
133	1	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	1	1	1	1	
134	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
135	–	1	–	2	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	
136	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	1	–	–	
137	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	
138	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	
139	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
140	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	
141	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	
142	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	
143	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
144	–	–	–	–	–	1	1	–	–	1	–	1	–	–	–	–	–	–	2	–	–	1	–		

No. of days after sowing 1–2 mm.	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y
145	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1
146	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2	1
147	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
148	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–
149	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	2	1
150	–	–	–	1	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
151	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
152	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–
153	2	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
154	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
155	–	–	–	–	–	–	–	•–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
156	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
157	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
158	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
159	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–
160	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–
161	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	–
162	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
163	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
164	–	–	–	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	2	1
165	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
166	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–
167	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
168	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	2	–	–	–
169	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
170	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
171	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
172	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
173	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
174	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
175	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
176	–	1	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
177	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	2
178	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
179	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–
180	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
181	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
182	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
											5 days blank														
188	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	2	1	–
189	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
190	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
											4 days blank														
195	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
196	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

After the 196th day there was no further germination day except one seed in set Y on the 207th day and one seed in set V and one in set Y on the 228th day.

In all these sets, intermittent germination was shown and a remarkable degree of constancy was exhibited. Germination commenced on the third day after sowing. The maximum was attained a few days later—approximately on the tenth day. It is remarkable that whereas 28 days after sowing the seeds had already reached a percentage germination averaging 60–80 %, the very high total percentage germination, namely 90–100 %, is obtained only after the seeds have been in conditions favourable to germination for a period of, in some cases, 100 to more than 200 days. The type of germination obtained remained constant, despite the fact that some tests were not carried out till the October after gathering the seed, while still others were made the following spring. A typical germination graph is shown in Fig. 1 (b). Further investigation is necessary, however, to determine whether the same type of germination graph

obtains with seed kept for more than one year after collecting. The behaviour of seeds sown immediately they are ripe requires further investigation.

It was considered desirable to ascertain whether differences in light intensity affect the type of germination of this species. Three pots, each containing 100 seeds, were set up as in the previous tests. One set was placed in the dark, a second set was subjected to the relatively bright light of a greenhouse during the day, and a third set was placed where the light intensity was low. Here again, the form of the germination graph for any one of the three tests did not deviate from the normal type. Intermittent germination in this species, therefore, does not appear to be affected by exposure to bright light or to darkness, although the germination extended over the longest period in the dark (193 days) and the shortest in the light (168 days).

Experiments were set up in November, and others in April. During November and December the average temperature of the laboratory was 50° F., the highest temperature recorded being 60° F. and the lowest 46° F. In the April experiments the temperatures during the day were considerably higher and more uniform, since the pots were kept in a heated greenhouse, the temperature of which was approximately constant at 60° F. The form of the germination graphs of the experiments set up in October did not however differ appreciably from that of the April experiments. Thus it appears that differences in temperature do not affect the type of intermittent germination.

An attempt has been made to investigate the cause of the intermittent germination observed. The problem has been to discover whether the delayed germination of a large percentage of seeds of this species is due to the relative impermeability of the testa in some of the seeds. Another possibility was that seeds, which germinate some considerable time after sowing, may contain immature embryos.

The testas of 300 seeds were abraded. This was done by rubbing each seed gently on fine sandpaper. The aim was to puncture the testa at the broader end of the seed, this being the end furthest away from the micropyle. The seeds were sown in sets of 100. 100 unfiled seeds were sown in a fourth pan as a control. The following results were obtained.

No. of days after sowing	A	B	C	Control
2	62 (62 %)	82 (82 %)	66 (66 %)	2 (2 %)
3	4 (66 %)	—	—	10 (12 %)
4	—	—	—	—
5	—	—	2 (68 %)	9 (21 %)
6	11 (73 %)	—	—	11 (32 %)
7	—	—	—	3 (35 %)
8	2 (75 %)	—	—	—
9–12		None		
13	—	—	—	5 (40 %)
14	—	—	—	—
15	2 (77 %)	—	—	—
16–18		None		
19	—	—	—	1 (41 %)
20	—	—	—	3 (44 %)
21	—	—	—	—
22	1 (78 %)	—	—	—

No further germination of the experimental seeds was obtained, but one control seed germinated on the 31st day, and germination of the controls continued at intervals thereafter.

It was found that even on the second day after sowing, a high percentage of the filed seeds had germinated (from 62–82 per cent.), whereas the percentage germination in the control experiment was only 2 per cent. in 2 days and 45 per cent. in 31 days. The technical difficulty of abrading the testa of 300 seeds as small as those of *H. guttatum*, in an exactly similar manner and to the same extent in every seed, will be appreciated. The fact that in two of the three sets of filed seeds a few germinated subsequent to the majority, can be explained by the warrantable assumption that the testas of these seeds were not abraded as deeply as were those germinating on the second day after sowing. The filed seeds which had not germinated by the 22nd day after sowing were concluded to have been badly damaged in the filing process.

These results render it highly improbable that intermittence is due to any appreciable extent to differences in the degree of maturation of the resting
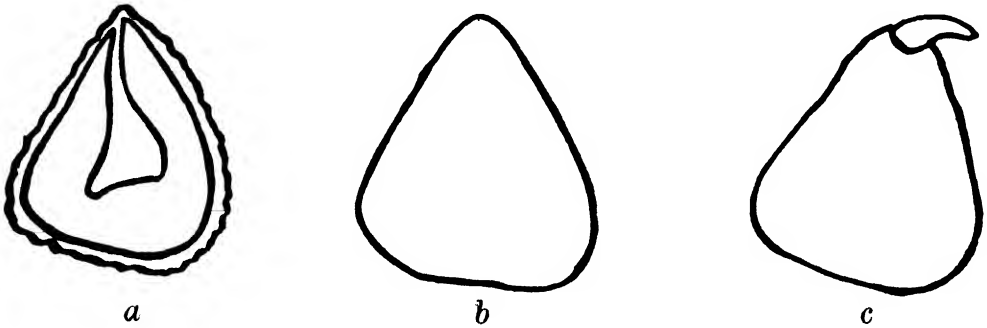
Fig. 2. *a* and *b*, "hard" and "soft" seeds after 48 hours soaking in tap-water; *c*, "soft" seed germinating.

embryos. On the other hand, the results strongly support the view that intermittence is bound up with the greater or lesser degree of permeability of the testa.

As a sequel to the filing experiments complete removal of the testa was attempted. The small size of the seed necessitated soaking before removing the testa. Seeds were soaked for 24 hours and then examined under a dissecting microscope. It was obvious that some of the seeds had swollen more than others. In the swollen seeds the outline of the embryo was not visible through the testa (Fig. 2 *b*). These seeds were soft and from them the testas could be removed with dissecting needles. The less swollen seeds were hard, and in these the well defined curved embryo could be seen through the testa. The testas of the hard seeds could not be removed without injuring the embryo (Fig. 2).

The testas were removed from 50 "soft" seeds, and the exposed embryos were set as usual on the surface of the sand and moistened with tap water. The embryo consisted of a radicle which lay flat against two cotyledons of the same length as the radicle. The seeds were assumed to have commenced germination when the radicle separated from the white cotyledons and turned

downwards. By this time the cotyledons had usually become yellow. Since the apparently simultaneous germination after filing might be attributed to an intermittent germination, in which however the whole sequence was passed through in a much abbreviated period, observations were made at hourly intervals so as to test this point.

Set at 11 a.m.	No. germinated	Percentage
12 midnight	2	4
1 a.m.	2	4
2 a.m.	16	32
3 a.m.	50	100

Thus 13 hours from the time of setting, germination commenced and 100 per cent. germination was recorded within 3 hours. Simultaneous germination was also obtained from a further batch of seeds similarly treated. These, however, only attained a total percentage of 80, the remaining 20 per cent. shrivelled up, probably due to injury during the removal of their testas. Thus with the removal of the testa intermittency disappears.

The embryos were found to differ in size but this did not differentiate them as regards the time taken to germinate.

Fifty soft seeds which had been soaked for 24 hours were planted in a pot, but the testas were not removed. A control of 50 seeds without testas was also set up.

Days after soaking	Days after sowing	Testas intact	Testas removed
2	1	0	49 (98 %)
3	2	23 (46 %)	—
4	3	11 (68 %)	—
5	4	3 (74 %)	—

Thus a much higher percentage of the "soft" seeds germinated within 5 days from the time of sowing than was found in the unselected seed batches first set up.

In time, hard seeds which were left soaking in water became soft, and the softened seeds were removed from day to day. The results are shown in the following table:

No. of days soaking	No. of hours soaking	No. of seeds removed
1	24	50
2	48	40
3	72	12
4	96	12
5	120	0
6	144	0
7	168	7
8	192	7
9	216	0
10	240	2

After soaking for 528 hours some seeds were still hard; 25 of these were then removed and planted. It will be seen from the table below that these very hard seeds are very slow in germinating. Germination was not inhibited by the long soaking in water since the soft seeds germinate quite well in water, producing healthy green cotyledons.

25 hard seeds soaked in cold water for 22 days (528 hours) then planted on sand over soil.

Days after beginning of soaking	No. of seeds germinating per day
23	1
24	0
⋮	
53	2
54	1
⋮	
63	2
⋮	
65	1
⋮	
100	8
⋮	
156	2

It would thus appear that there is a physiological dimorphism in respect to the permeability of the testa among the seeds of *H. guttatum*. Those seeds having the higher degree of permeability germinate within a few days (about five) of sowing, when in conditions favourable to germination, while the impermeable seeds germinate only when the testa has become permeable, their germination extending over a prolonged period up to 228 days.

Some seed was soaked in water, and after 48 hours the "soft" seeds were removed. Then 100 "hard" seeds were planted. Another batch of seed was soaked for 3 hours and then a second set of "hard" seeds was planted. Intermittent germination was exhibited by both batches of "hard" seed as shown below.

Days after sowing	Set A 48 hours soaking	Set B 3 hours soaking	Days after sowing	Set A 48 hours soaking	Set B 3 hours soaking
2	–	6	18	1	–
3	–	3	19	–	12
4	–	–	20	1	–
5	10	13	21–23	None	
6	3	8	24	1	–
7	4	8	25	2	–
8	3	9	26	3	
9	–	3	27	1	5
10	7	–	28	–	1
11	4	–	29	–	5
12	12	2	30	–	5
13	–	–	31	–	1
14	–	4	32–33	None	
15	6	1	34	7 (71 %)	–
16	1	–	35–36	None	
17	5	4	37	–	1 (91%)

An attempt was made to increase the permeability of the testas by means of chemical treatment. Two batches of seeds were soaked in concentrated sulphuric acid for 5 min. and 30 min. respectively and then thoroughly washed in water for one hour. Control batches were set up, but were soaked in tap water for 1 hr. 5 min. and 1 hr. 30 min. respectively. The seeds were afterwards transferred to four germination pans.

Intermittent germination was still exhibited in each batch. Treatment with acid, therefore, had not increased the permeability of the testa, but since 100 per cent. germination was ultimately obtained in the seeds soaked in acid for 30 min. such treatment had not injured the embryos. The result of treatment with acid for a longer period has yet to be investigated.

The problem of differential permeability resolves itself into two factors— Does the mere increased permeability of the testa to moisture and salts in solution hasten germination, or does increased permeability enhance germination by facilitating gaseous exchange between the embryo and the atmosphere? It is obvious that when the testa is punctured the supply to the embryo of both water containing salts in solution and gases is materially increased, and under such conditions, simultaneous germination was obtained.

To elucidate this point, seeds have been germinated in an atmosphere containing an increased partial pressure of oxygen. 100 seeds with their testas intact were planted on sterilised sand in a petrie dish, and moistened with tap water. In this experiment the underlying layer of soil was omitted, since decomposition of the humus therein would increase the partial pressure of CO_2 in the atmosphere around the petrie dish, and this was not desirable. The dish was placed in a container connected with a gasholder containing oxygen and air in the ratio of 50 per cent. oxygen to 50 per cent. air. This enriched atmosphere was then passed slowly through the container. The gasholder was recharged with the mixture each morning. This experiment was continued for 11 days. Control batches of 100 seeds each were prepared on sand in petrie dishes and kept exposed to the atmosphere. It was found that the rate of germination was not increased by increasing the oxygen content of the surrounding atmosphere.

| | 50 % O_2 : 50 % air. Daily germination | | Control | |
Days after sowing	Appearance of radicles	Appearance of plumules	Daily appearance of radicles	Daily appearance of plumules
3	—	—	1	—
4	—	—	6	—
5	10	1	37	5
6	—	—	—	—
7	2	11	5	41
8	4	2	9	9

It seems, therefore, that germination in *Helianthemum guttatum* is conditioned by the rate at which the testas become permeable to water and salts in solution. It is clear that the high proportion of germinations in the first few days is due to the "soft" seeds whilst the collective graph for the total 2500 germinations suggests the possibility of continuous germination amongst the "hard" seeds if the number of germinations were vastly increased. The reasons for the wide variation amongst the latter remains however obscure.

Summary.

1. An account of the type of germination of seeds of *Helianthemum guttatum* Miller is given.

2. Intermittent germination was found to be constantly exhibited.

3. The results from 25 sets of 100 seeds each showed a remarkable constancy in the type of germination "curve."

4. The very high percentage germination in this species (90–100 per cent.) was not attained till 200–300 days after sowing, but the highest germination occurs about the tenth day.

5. Differences in light intensity do not appear to modify appreciably the type of the germination graph.

6. The cause of the intermittent germination was investigated, and it was found that when the testas were abrased, simultaneous germination was produced.

7. Hourly determinations on seeds from which the testas were completely removed showed that the simultaneous character of the germination observed was real and not merely apparent.

8. It was found that in any batch of seeds investigated, some were "soft" and some "hard." Prolonged soaking in water was found to "soften" hard seeds.

9. "Soft" seeds germinated within a few days after sowing whilst the "hard" seeds germinated only after their testas had become permeable. Thus the degree of permeability of the testa determines the rate of germination of the seed.

10. Increased partial pressure of oxygen in the atmosphere in which seeds were germinated, does not appear to accelerate the rate of germination.

11. The rate of germination in *Helianthemum guttatum*, therefore, seems to be conditioned by the rate at which the testa is rendered permeable to water and salts in solution. Hence the relatively constant form of the germination graph probably represents the variation curve for the degree of permeability of the testas. Intermittency thus appears to be conditioned by two factors. The physiological dimorphism of the seeds ("hard" and "soft") and the very wide range of variability as to permeability of the testa exhibited by the "hard" seeds.

REACTION OF PLANTS TO THE DENSITY OF SOIL[1]

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(With one Figure and four Graphs in the Text.)

(a) INTRODUCTION.

IN 1925 Prof. E. J. Salisbury, while considering the structure of woodlands (9), recognised the significance of the mechanical factor of the soil as exercising an important influence on the rhizomes of woodland plants.

Some studies have also been made by Eden and Maskell (4) at Rothamsted for winter wheat and a correlation found between the soil resistance and the number of plants surviving the winter and the percentage of plants that tillered. Keen (7) is inclined to attribute the better development of the root system, observed in coarse sand by Hall, Brenchley and Underwood (5) in their experiments with lupins grown in sand and silt, to the absence of the mechanical factor (in coarse sand) rather than to differences in diffusion of oxygen as the authors suggested.

Perusal of the ecological literature makes it clear that this factor in relation to plant growth has been almost entirely neglected in comparison with other biotic, edaphic and climatic factors on which a vast literature already exists.

It is proposed to consider in this paper the reaction of plants to the density of the soil with special reference to root systems of both monocotyledonous and dicotyledonous plants.

The importance of the study of soil texture to agriculture has been pointed out by Weaver (12) in *Root Development of Field Crops*, and by Keen in *Physical Properties of the Soil*. Haines and Keen (6) have measured the resistance of the soil to ploughing and its relation to moisture and manures at Rothamsted by means of the dynamometer.

To supply an answer to the problem in hand some experimental work in the laboratory supplemented by field observations was carried out. The experimental work consisted of an examination of the physical properties of a selected soil under mechanical compression as regards its water capacity, differences in pore space, resistance to flow of water and penetrability, and culture experiments. Field observations were made on the length and thickness of internodes of rhizomes of *Mercurialis perennis* in soils of varying texture.

Throughout the discussions that follow the terms "compressed," "intermediate" and "loose" are employed to denote three densities of the selected

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[1] Part of thesis approved for the Degree of Master of Science in the University of London.

soil that was used in the experiments. The soil was completely air dried and thoroughly sifted before compressing in iron tubes. Uncompressed samples are termed "loose," samples compressed as much as possible by dense packing with a ramrod and a mallet are termed "compressed," and the samples less compressed are termed "intermediate." Evidence will be afforded in the sequel to show that the density of the samples in each category was relatively uniform.

(b) Determination of pore space.

A suitable soil, which would yield three distinct grades on compression, having been selected, the physical properties of the soil were studied.

It is obvious that soils contain in addition to the mineral constituents of the original rock and organic material a certain amount of air and water between their individual particles. The texture of the soil determines the volume of the pore space, the smaller the size of the particle the larger the volume of the pore space, chiefly because the finer the constituent particles the less readily do they pack into the condition of the maximum compression.

The determination of pore space is of twofold importance. Firstly it will help to show the uniformity of different samples subjected to different degrees of compression, and secondly it is of great significance to the study of culture experiments, as the resistance to penetration through different grades of soil by the root will depend on its capacity to displace the particles around it, i.e. to pack them more tightly in its immediate vicinity.

A known volume of air-dried and sifted soil was taken and its weight subsequently determined. The air from this sample was expelled by alcohol and the volume of air space determined from the volume of alcohol both by weighing and volumetrically, using one as a check upon the other.

The same method was employed for the compressed and intermediate samples when they were compressed to their respective volumes. The volume of pore space was expressed as a percentage.

The results are set out in Table I. It will be noticed that actually the volume of pore space in the compressed soil is not so small as might be anticipated from the reduction in total volume of the soil as compared with the uncompressed soil. In other words the packing of the soil particles in the compressed soil is relatively not so good as in the loose soil.

By a reference to the same tables the absolute means are found to be 42·37 per cent. for compressed soil, 46·38 per cent. for intermediate soil and 51·94 per cent. for loose soil. And the range in the same order is 39·98–43·76, 42·81–48·03 and 51·00–52·87. The range is relatively greater in the intermediate grade, which is in accordance with expectations as compared with compressed or loose soils. Though the density is increased by 12 and 21 per cent. the decrease in pore space is not exactly proportional, being respectively 11 and 18·5 per cent. As the method of compressing the soil by hand might produce variable results it is important to note that the determinations of

pore space show that the different samples in the same category of compression (i.e. compressed or intermediate) were relatively uniform, and even the extremes for the two degrees of compression show very slight overlap.

Table I. *Pore space. Artificial soil, air dried.*

Compressed		Intermediate		Loose	
Density	% pore space	Density	% pore space	Density	% pore space
1·37	43·76	1·27	48·03	1·13	52·87
1·36	43·48	1·28	47·63	1·12	52·86
1·35	43·23	1·26	47·60	1·14	52·76
1·36	43·16	1·29	47·34	1·13	52·73
1·36	43·12	1·29	47·29	1·12	52·54
1·36	43·08	1·28	47·29	1·12	52·52
1·37	42·91	1·26	47·11	1·12	52·47
1·36	42·87	1·27	46·99	1·14	52·45
1·36	42·83	1·25	46·96	1·13	52·38
1·39	42·75	1·26	46·94	1·12	52·36
1·36	42·74	1·25	46·93	1·13	52·35
1·36	42·71	1·28	46·85	1·13	52·30
1·40	42·67	1·27	46·77	1·13	52·29
1·37	42·63	1·25	46·77	1·14	52·27
1·36	42·58	1·29	46·69	1·13	52·13
1·39	42·51	1·28	46·60	1·13	51·96
1·36	42·49	1·28	46·58	1·12	51·87
1·36	42·49	1·28	46·57	1·13	51·86
1·37	42·36	1·28	46·53	1·15	51·85
1·41	42·34	1·29	46·48	1·14	51·85
1·39	42·31	1·28	46·44	1·13	51·83
1·36	42·31	1·27	46·33	1·13	51·80
1·37	42·28	1·29	46·30	1·15	51·71
1·36	42·28	1·29	46·29	1·12	51·66
1·36	42·15	1·27	46·18	1·13	51·55
1·41	42·06	1·27	46·18	1·13	51·54
1·37	42·03	1·27	46·08	1·13	51·59
1·41	41·84	1·28	46·01	1·12	51·41
1·39	41·79	1·27	45·75	1·15	51·32
1·39	41·61	1·30	45·56	1·13	51·18
1·39	41·29	1·28	45·34	1·13	51·09
1·36	41·25	1·29	44·77	1·14	51·07
1·36	41·16	1·25	42·83	1·13	51·54
1·39	41·08	1·30	42·81	1·13	51·04
1·40	39·98	—	—	1·13	51·00
Mean 1·37	42·37	1·27	46·38	1·13	51·94
Per cent. 121	81·5	112	89	100	100
Range	39·98–43·76		42·81–48·03		51·00–52·87

(c) Water capacity and flow of water.

The three grades of soil samples were allowed to absorb water from below to their maximum capacity, and this amount of water was determined. The water capacity against the height of soil in tubes is shown in Table II. As the tubes of equal diameters were used in all the three cases, the volumes will be inversely proportional to densities.

Table II gives 36·11 c.c. to be the mean water-holding capacity of compressed soil with a range of 33·15–37·40: 41·84 c.c. to be the mean water-holding capacity of intermediate soil with a range of 38·84–44·95; and 50·20 c.c. to be the mean water-holding capacity of loose soil with a range of 46·80–52·61.

If the densities for loose, intermediate and compressed soils are expressed as 100 : 113 : 123, then the corresponding water capacities can be expressed as 100 : 83·34 : 71·93, or if the density of the intermediate soil is increased by 13 per cent. the water capacity is decreased by 16·66 per cent., and if the density of the compressed soil is increased by 23 per cent. its water capacity is decreased by 28 per cent. The lowering of the water capacity in the compressed soil agrees fairly well with increase in density and reduction in the pore space. It is also clear from Table II that the values for each grade of soil are quite distinct and do not overlap at all. The range is comparatively wide in loose and intermediate grade and can be easily explained by the relatively irregular and disorderly arrangement of the soil particles in those grades, as compared with compressed. Further if we are considering the same volume of soil in each case, i.e. volume equivalent to 1 cm. of soil in height in the tubes, we find that the water capacity works out to be 5·39 c.c. for compressed soil, 5·80 c.c. for intermediate soil and 6·04 c.c. for loose soil.

Table II. *Water capacity. 100 gm. of air-dried and sifted soil used in each case.*

Compressed		Intermediate		Loose	
Height cm.	Water capacity c.c.	Height cm.	Water capacity c.c.	Height cm.	Water capacity c.c.
6·8	37·40	7·4	44·95	8·2	52·61
6·8	37·23	7·4	43·70	8·3	52·14
6·7	37·23	7·4	43·14	8·3	51·97
6·7	37·12	7·4	43·10	8·3	51·86
6·8	37·07	7·2	42·85	8·3	51·57
6·8	37·04	7·4	42·35	8·3	51·46
6·8	36·95	7·4	42·32	8·3	51·40
6·8	36·77	7·4	42·30	8·3	51·09
6·8	36·68	7·4	41·69	8·2	50·80
6·7	36·40	7·4	41·65	8·3	50·69
6·8	36·18	7·4	41·43	8·2	50·58
6·5	35·88	7·0	41·43	8·3	50·32
6·6	35·67	7·4	40·80	8·2	48·91
6·7	35·65	7·2	40·62	8·3	48·47
6·7	35·54	7·2	40·50	8·2	48·33
6·6	34·30	7·0	39·80	8·2	47·42
6·8	33·80	7·3	39·78	8·2	47·32
6·4	33·15	7·1	38·84	8·1	46·80
Mean 6·7	36·11	7·3	41·84	8·3	50·20
Range 6·4–6·8	33·15–37·40	7·0–7·4	38·84–44·95	8·1–8·3	46·80–52·61
Height of 1 cm. or vol. 11·34 c.c.	5·39		5·8		6·04

These data show that increased density as such does not in itself greatly affect the water-holding capacity. In other words the plants grown on soils of the same type but of different densities are more likely to be influenced by the marked differences in mechanical conditions than by the relatively slight differences in water-retaining capacity.

Some idea of the rate of absorption of water by these soils may be of interest. Much work has been done in this connection with different kinds

of soils, such as sands, loams and clays, both in America and England. Bear (1) regards the medium-textured soils such as loams to be the best for the movement of water and the height to which it will rise. For the heights that I have used for my experiments with the selected soil under different compressions the data suggest that the movement of water from below upwards is retarded to some extent by compression which may or may not be of any significance for these heights. The average time taken to rise through unit heights in loose soil was 13·3 min., in intermediate soil 17·5 min. and in compressed soil 20·4 min. Thus with the rate of flow employed the water-supplying power of the compressed soil is only about two-thirds of that of the loose soil. In situations where transpiration is high the degree of compactness of the soil may well play a considerable part in restricting the water supply by affecting the rate of flow.

Table III. *Rate of flow of water. Time 30 min.*

Compressed		Intermediate		Loose	
Height cm.	Amount of water in c.c.	Height cm.	Amount of water in c.c.	Height cm.	Amount of water in c.c.
6·8	15·54	7·4	44·91	8·3	192·72
6·8	13·62	7·4	40·97	8·3	187·17
6·8	11·14	7·4	36·26	8·3	184·91
6·8	11·09	7·2	35·09	8·3	180·62
6·8	10·67	7·3	34·80	8·3	168·12
6·8	10·56	7·4	32·03	8·3	160·18
6·7	10·53	7·4	32·01	8·3	157·00
6·7	8·97	7·4	31·37	8·2	154·62
6·8	8·95	7·0	25·61	8·2	152·17
6·6	7·10	7·4	24·67	8·2	150·14
6·7	6·76	7·4	24·00	8·3	145·57
6·8	6·19	7·1	23·93	8·1	128·42
6·7	5·72	7·2	23·30	8·2	118·59
6·7	4·94	7·4	22·30	8·2	109·65
6·6	4·20	7·4	21·05	8·2	102·47
6·5	4·15	7·0	20·25	8·3	100·37
6·4	3·25	7·4	20·07	8·2	98·18
		7·2	16·09	8·2	91·67
Mean 6·7	8·38	7·3	28·26	8·25	143·47
Range 6·4–6·8	3·25–15·54	7·0–7·4	16·09–44·91	8·1–8·3	91·67–192·72
Height of 1 cm. or vol. 11·34 c.c.	1·25		3·87		17·3

Water was forced through the samples which had absorbed water to their maximum capacity from a height of 1 m. to determine the amount of water passing through the samples in a known time. Equal quantities of air-dried and sifted soil were used in each case. Table III gives the results obtained. It will be at once noticed as with water-capacity experiments that the values obtained are remarkably distinct for each grade of the soil. The mean for compressed soil is 8·38 c.c. with a range of 3·25–15·54, for intermediate soil the mean is 28·26 with a range of 16·09–44·91, and for loose soil the mean is 143·47 c.c. with a range of 91·67–192·72. The table very clearly shows the resistance to flow of water offered by the increase in density. The amount of

water passing through unit height would be 1·25 c.c. in compressed soil, 3·87 c.c. in intermediate soil and 17·3 c.c. in loose soil. Clearly this resistance to flow with increasing compactness of a soil will become more significant as the rate of transpiration increases, and the more compact the soil the greater the danger of permanent wilting.

(d) PENETRABILITY.

This was determined both on the three grades of the selected soil as well as on natural soils, viz. sand, clay and loam. The effect of moisture on penetrability was also studied. The apparatus used was similar to that used by Prof. Salisbury in his studies of woodlands ((10), pp. 345–6) with slight modifications.

Table IV gives the relative penetrabilities of artificial soil, sand and clay under conditions of similar water content, i.e. air dried.

Table IV. *Relative penetrabilities of sand, artificial soil and clay*
(air dried and sifted) (2 divisions = 1 cm.).

	Medium sand div.	Artificial soil div.	Clay div.
	6·24	4·59	3·48
	6·10	4·25	3·43
	6·09	4·12	3·33
	6·03	4·06	3·32
	6·01	4·03	3·30
	5·94	4·02	3·27
	5·92	4·00	3·13
	5·83	3·99	3·11
	5·78	3·99	3·11
	5·40	3·95	3·09
Mean	5·93	4·10	3·26
Or	1	0·69	0·55

Only averages of each sample are shown in Table IV, which shows quite clearly the difference in the penetrability of these soils. If the penetrability of sand be expressed by unity then the penetrabilities of artificial soil and clay can be expressed as 0·69 and 0·55 respectively, or in other words if we are considering the same species of plants growing on these soils the root should encounter nearly twice as much resistance from clay and about one and a half times as much resistance from artificial soil as compared with sand. Knowing as we do that sand has the largest individual particles and clay the smallest, the interspaces enclosed by the sand are also much larger as compared with clay. Under the force of penetrating roots the particles of sand nearest to the root will be easily displaced and allow easier passage to the root and consequently less expenditure of energy as contrasted with clay. Besides there not being much room for displacement of the particles in clay the frictional resistance will soon become significant and may make it extremely difficult for the root to make its way by displacing the particles. Plants grown in sand and clay show remarkable differences in the lengths of

roots. Even those plants which are grown in the same soil but of different texture as sand and silt show differences in root growth. Experiments of Hall, Brenchley and Underwood (5) with lupins are of special interest in this connection. They recorded a larger root development in materials such as coarse sand and kaolin than in fine sand and silt. Considering the differences in the penetrabilities of different soils and of the same soil under different compressions (to be studied below) it seems reasonable to infer the great importance of density of soil on the development of root systems.

The penetrabilities of the selected soil are given in Table V under different mechanical compressions. Twenty different samples were taken in each case and ten readings taken of each sample.

Table V. *Penetrabilities. Garden soil, air dried and sifted.*

Compressed		Intermediate		Loose	
Density	Penetrability	Density	Penetrability	Density	Penetrability
1·32	2·86	1·24	3·14	1·22	3·99
1·32	2·68	1·24	3·38	1·21	4·20
1·31	2·92	1·24	3·10	1·21	3·94
1·28	2·82	1·24	3·40	1·20	4·16
1·28	2·76	1·23	3·38	1·20	4·29
1·28	2·81	1·23	3·14	1·20	4·19
1·27	2·78	1·22	3·18	1·19	4·13
1·27	3·08	1·22	3·26	1·18	4·41
1·27	2·94	1·22	2·96	1·18	3·98
1·27	2·86	1·21	3·02	1·18	4·41
1·27	3·08	1·21	3·54	1·18	4·11
1·26	2·82	1·21	3·36	1·18	4·30
1·26	2·78	1·21	3·18	1·17	3·96
1·24	2·98	1·21	3·12	1·17	4·03
1·24	3·00	1·20	3·86	1·17	4·89
1·23	2·78	1·20	2·92	1·17	4·12
1·22	2·96	1·20	3·46	1·17	4·00
1·22	2·90	1·19	3·44	1·17	4·34
1·21	3·18	1·19	3·62	1·17	4·27
1·21	3·16	1·16	4·26	1·16	4·91
Mean 1·26	2·92	1·21	3·12	1·18	4·23

The table shows the means of all the samples which are: for compressed soil 2·92, for intermediate soil 3·12 and for loose soil 4·23; also the corresponding densities which are 1·26 for compressed soil, 1·21 for intermediate soil and 1·18 for loose soil. To put the results in a more convenient form we would refer to the penetrabilities of loose, intermediate and compressed soils as 100 : 77·5 : 69·0 and corresponding densities as 100 : 102·5 : 106·7. The part played by frictional resistance between individual particles as they are brought closer together in offering resistance to penetrability will be clear. When the density is increased from 100 to 102·5 the penetrability decreases from 100 to 77·5, but if the density is further increased to 106·7, the penetrability is only reduced to 69·0. Thus the resistance encountered by the roots in pushing through a soil will not be one of direct proportion as the density is increased or the pore space reduced. The degree of penetration will depend upon the capacity of the root or any other foreign object to pack the particles more

tightly in its vicinity. As the particles are brought closer together the frictional resistance between the particles will increase, and might become so great at a certain stage as to prevent any further displacement, thus checking the penetration of the root into the soil.

The penetrabilities of the experimental soil under air-dried conditions have already been given in Table V. In Table VI are given the penetrabilities of similar soil at three different water contents.

Table VI. *Penetrability of experimental soil under different water contents*
(2 *divisions* = 1 *cm.*).

Water contents... 29·7 %	16·4 %	7·07 %
div.	div.	div.
8·4	6·3	5·1
8·3	6·2	5·0
8·2	6·1	4·9
8·1	6·1	4·9
7·9	6·0	4·8
7·8	5·9	4·7
7·8	5·7	4·6
7·7	5·5	4·6
7·3	5·2	4·6
7·1	5·2	4·5
Mean 7·8	5·8	4·7

The averages of ten readings taken on each of the ten samples are given in Table VI. The table shows how the penetrability increases or resistance from the soil decreases with the increasing moisture content. By decreasing the moisture content from 29·7 to 16·4 per cent. the penetrability falls from 7·8 to 5·8, and by decreasing the moisture content from 16·4 to 7·07 per cent. the penetrability further falls from 5·8 to 4·7. In Table V we had occasion to notice the penetrability of air-dried soil to be 4·23, so that my results suggest a very clear correlation between the penetrability of soil or resistance from the soil and moisture content.

In a recently published book, *The Physical Properties of the Soil*, Keen (8) observes that no definite correlation has been established between soil resistance and moisture content in experiments with the dynamometer at Rothamsted. My observations as outlined above and in the field have convinced me that a very significant correlation exists between penetrability and moisture content. The fact that in ploughing the soil is raised by the plough iron towards the free upper surface whereas in penetrability determinations the soil is supported on all sides may well account for the divergence of the results.

The correlation between water content and penetrability may well be due to a lubricating effect of the water when the soil particles are more tightly packed by the penetrating root.

(e) Culture experiments—beans.

Three series of pots were prepared. The pots in each series contained equal amounts of sifted soil compressed to an equal degree. In one set the soil was compressed, in the second set the soil was compressed slightly and the third contained soil which was not compressed at all. Equal number of bean seeds (*Vicia faba*) were put in each pot and covered with an equal amount of the same artificial soil. The pots were affected equally by daily changes of light and temperature, and were given equal amounts of just sufficient water from day to day. In complying with these conditions it will be seen that the seeds in the pots were sown in the soils of the same physical and chemical characters with only the differences consequent upon the differing densities of the soils, the chief differences due to density being mechanical resistance to root penetration, increased resistance to flow of water, lowering of water capacity and diminished aeration.

Table VII. *Germination of seeds.*

Culture No.	Soil	Seeds planted	Seeds germinated	% of germinated seeds	No. of seedlings dying after germination	Apparent cause of mortality after germination
I. 4 seeds in each pot	Loose	12	11	91·6	None	—
	Intermediate	12	12	100	1	Soil
	Compressed	12	10	83·3	None	—
II. 3 seeds in each pot	Loose	9	8	88·8	None	—
	Intermediate	9	8	88·8	None	—
	Compressed	9	7	77·7	2	Soil
III. Single seed in each pot	Loose	2	2	100	None	—
	Intermediate	2	2	100	None	—
	Compressed	2	1	50	None	—
IV. Single seed in each pot	Loose	3	3	100	None	—
	Intermediate	3	3	100	1	Fungus
	Compressed	3	3	100	?	Soil
V. Single seed in each pot	Loose	3	3	100	1	Fungus
	Intermediate	3	3	100	None	—
	Compressed	3	3	100	1	Soil

In due course the seeds began to germinate. The time taken by the seeds to germinate was very irregular. Sometimes the seeds germinated first in the loose soil, while at other times in compressed or intermediate soils. But the percentage of seeds germinating was different in different series, as also the number of plants obtained from the successful seeds, for some died soon after germination. The schedule of the germination of seeds is given in Table VII. It will be seen that the percentage of seeds germinating in the first three cultures is the lowest in the compressed soils, being 83·3, 77·7 and 50 per cent., as against 91·6, 88·8 and 100 per cent. in loose and 100, 88·8 and 100 per cent. in the intermediate pots. Whether this variation in the germination of seeds is due to unequal air contained in the pore space consequent on mechanical compression or the density of soil has any direct effect cannot be accounted for

at present. To me it seems that this variation is not due to differences in aeration, as intermediate pots show better results as compared with the loose pots in all the cultures. Taking all cultures together 93·1 per cent. germinated in loose soils and 82·7 per cent. in the compressed soils, but it is doubtful whether this difference can be regarded as significant although it suggests that compression may reduce the percentage of germination.

The direct effect of the density of soil is better seen on seeds which have already germinated. When the radicle grows it naturally must penetrate through the substratum to discharge the future functions of the root to which it will give rise. But it is prevented in some cases, as actually observed by the hardness of the substratum. It was observed in cultures IV and V that the radicle attained a length of 5–6 cm., gave out rootlets, wandered on the surface of the soil and withered when it could not push through the soil in the case of compressed sets. Similar conditions were found in cultures I and II. One plant in intermediate soil (culture IV) and one in loose soil (culture V) were attacked by fungus which could be easily detected. In cultures IV and V which were carried out in 1931 it was observed that seeds were actually lifted 2 or 3 cm. above the soil in compressed and intermediate soils, while the radicle was struggling hard to push through the substratum.

The length of the shoot was measured from day to day, total growth being plotted against the number of days. The accompanying Graph 1, in so far as the rate of growth is concerned, shows no appreciable differences, but when the plants were cut the tops showed interesting results.

The mean height in culture I for loose soils was 35·0 cm., for intermediate soils 38·7 cm., and for compressed soils 28·9 cm. In Culture II the mean height for loose soils was 39·0 cm., for intermediate soils 31·5 cm., and for compressed soils 37·2 cm. Finally in culture IV the mean height for loose soils was 33·5 cm., for intermediate soils 27·3 cm. and for compressed soils 33·3 cm. The range for all the cultures was for compressed soils 19·8–48·0 cm., for intermediate soils 19·0–44·1 cm. and for loose soils 22·4–52·2 cm. These have been shown in Graph 3.

If the results of separate cultures are now compared it will be seen that sometimes the tops show a better growth in compressed and intermediate soils, at other times in loose soils. The results on the whole tend to indicate a greater dispersion in the loose and compressed soils. But the important point that these cultures appear to have revealed is that there is no significant difference in the growth in height of plants rooted in compressed and loose soils.
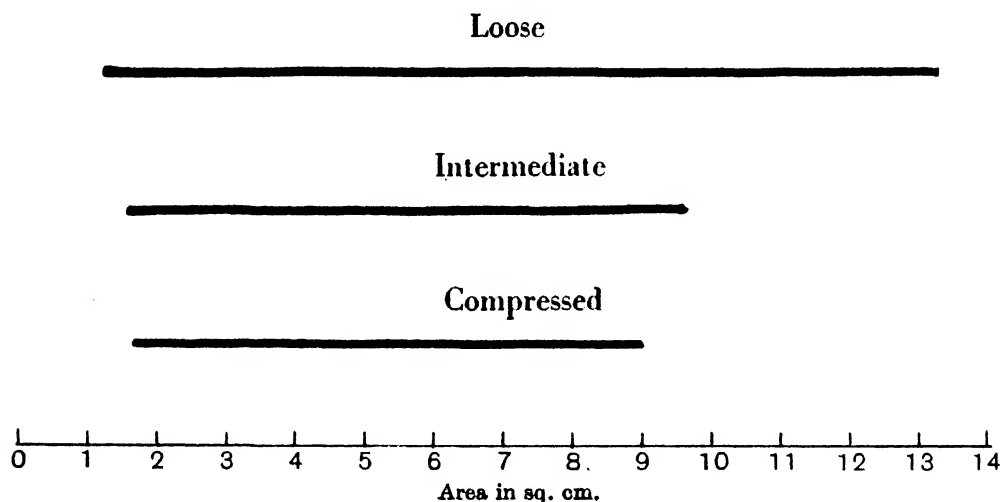
If we now turn to examine the area of assimilatory organs of the plants in different grades of the same soil we find that the leaves also exhibit no marked and constant differences. The total assimilatory area in different cultures for loose soils was 48·51, 39·67, 26·45 and 25·73 sq. cm., for intermediate soils 29·21, 28·24, 27·32 and 19·67 sq. cm., and for compressed soils 36·01, 32·08 and 22·66 sq. cm. The tables giving the area of each leaf of plants
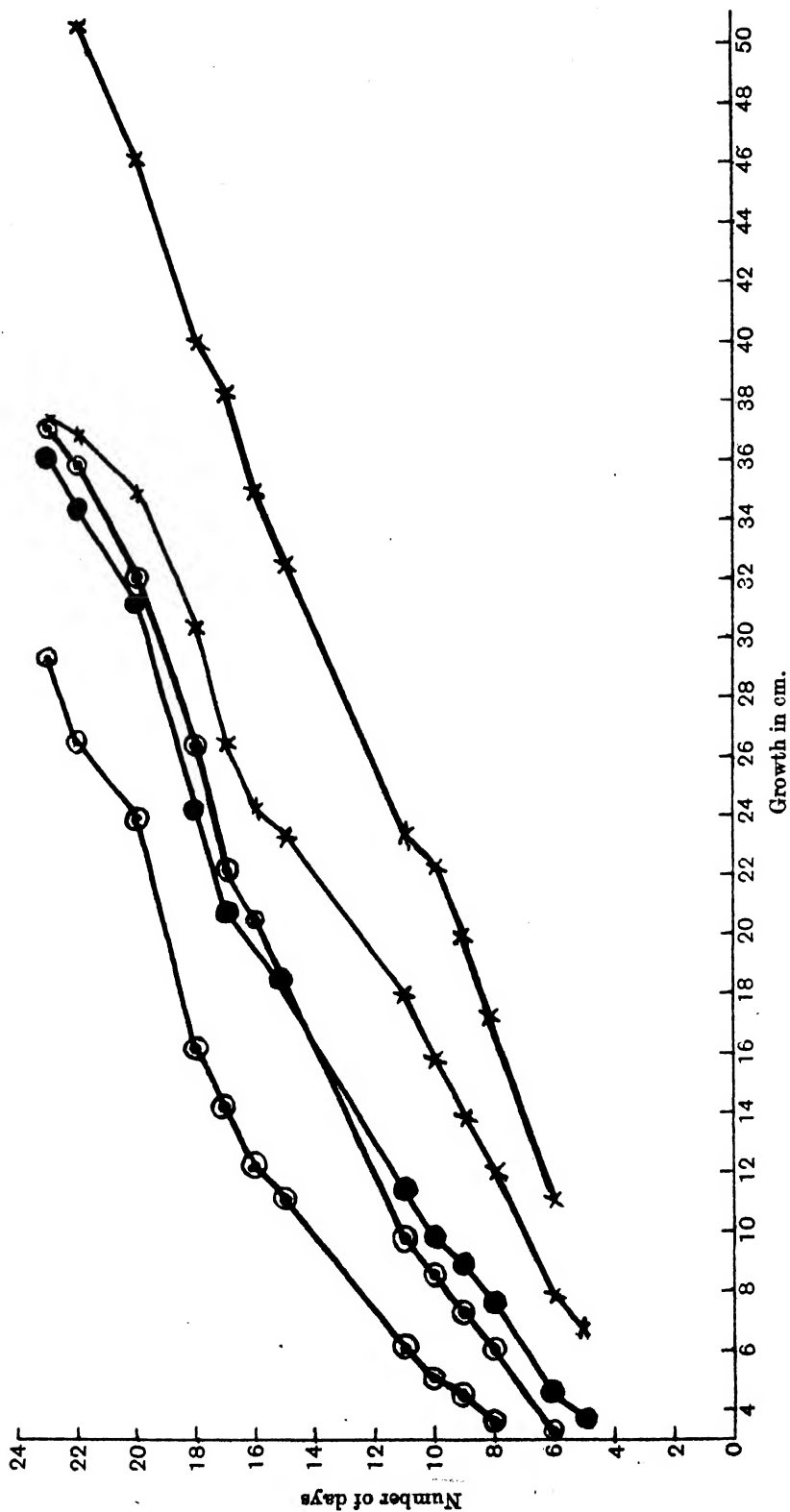
GRAPH 1. Rate of growth of beans. Culture III. × loose soil; ⊙ intermediate soil; ● compressed soil.

in cultures III and IV have been omitted, as they would occupy much unnecessary space; however, the dispersion in the area of leaves on different soils is shown in Graph 2, which gives only the lower and upper limits on each soil. They are for compressed soil 1·62–9·02 sq. cm., for intermediate soil 1·58–9·64 sq. cm., and for loose soil 1·24–13·29 sq. cm. It would then appear that so far as powers of assimilation are concerned, and in so far as lack of aeration in the soil may be compensated by leaf area, the plants in the three densities of soils are more or less equally conditioned.

The underground organs on examination offer a striking contrast to the comparative similarity of development of the aerial organs already noted. Not only a difference in size and length of the roots but interesting differences in the form and distribution of the underground organs are quite noticeable.

Loose

Intermediate

Compressed

```
 L____L____L____L____L____L____L____L____L____L____L____L____L____L
 0    1    2    3    4    5    6    7    8    9    10   11   12   13   14
```

Area in sq. cm.

GRAPH 2. Area of assimilatory organs (beans). Cultures III and IV. (Showing range.)

In general the roots in the compressed soils tend to take a superficial and shallow distribution with the laterals arising from the main root in a confused order, appearing like a tangled mass, as contrasted with those in the loose soils in which the main root is very long and gives out laterals on both sides in regular order. The radicle stops short in compressed soils, not growing more than 3 or 4 cm. The main root in this case has also been observed to divide. This check in the elongation of the main root is, to all appearance, the result of the considerable resistance exercised by the soil on the underground organs. The morphological features of the underground organs are considered in detail below. The mean lengths of the main roots in various cultures for loose soils are 42·5, 34·1, 22·2, 22·1, 21·2, 18·1 and 17·4 cm., for intermediate soils 22·4, 21·0, 17·6, 14·9, 12·4, 7·7 and 2·1 cm., and for compressed soils 11·6, 6·3, 5·2, 2·4, 2·2 and 1·8 cm. It will be seen from Graph 3 that in contrast with the tops the roots show a much wider range in lengths. The range in the lengths

of roots in all the cultures on compressed soil was 1·8–14·9 cm., on intermediate soil 2·1–22·4 cm., and on loose soil 12·4–42·5 cm. (Graph 3). The lengths of the main root in loose soils can thus attain from about ten to twenty times the length of those in the compressed soils.

The mean thicknesses or diameters of roots in cultures I and II in loose soils were 1·01 and 1·06 mm., in intermediate soils 1·18 and 1·33 mm., and in compressed soils 1·28 and 1·37 mm. In cultures III and IV the mean diameters for loose soils were 2·0, 2·0, 2·5 and 2·5 mm., for intermediate soils 3·4, 6·0, 1·9 and 2·0 mm., and for compressed soils 4·9, 4·5 and 4·5 mm. The same is

ROOTS   TOPS

Compressed

Intermediate

Loose
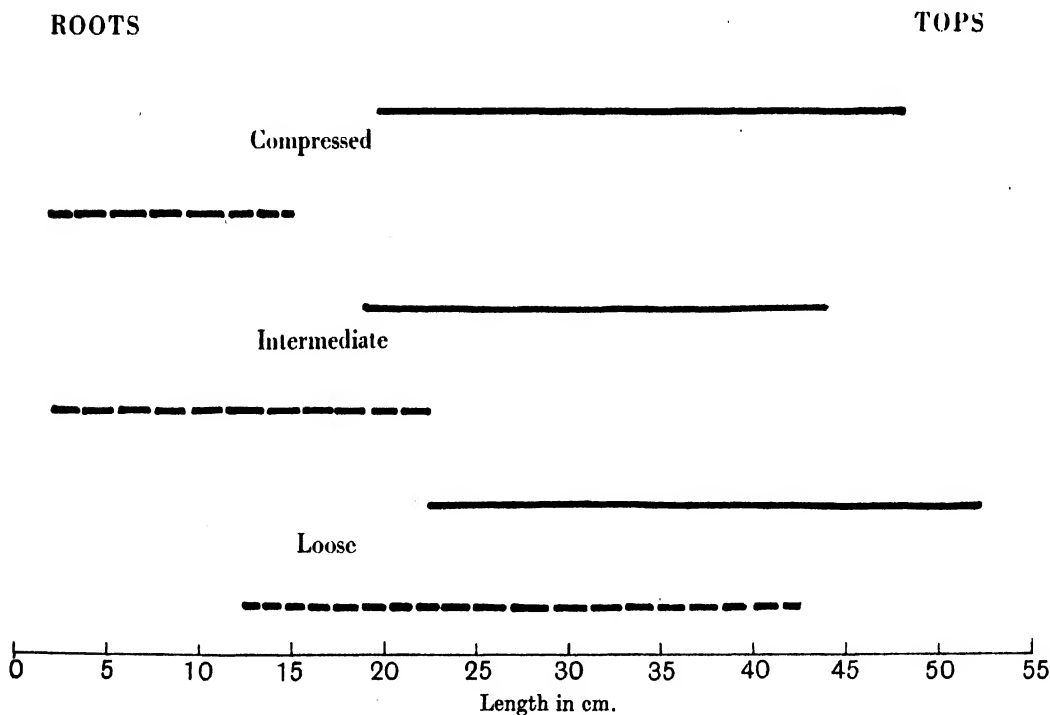
GRAPH 3. Lengths of tops and roots (beans). Cultures I–IV. (Showing range.)

true of laterals. So that the data given above with regard to the thickness of roots, based on hundreds of measurements in each case, clearly show that roots are thicker in compressed soils than in loose soils. There was a copious development of root hairs on the roots in all the soils of different densities. It is generally known that plants grown in badly aerated soils tend to lack root hairs. Also no traces of any kind of aerating tissue which might go to suggest the influence of differential aeration were found in the anatomy of the root. Thus there were no obvious morphological or anatomical signs of deficient aeration in the compressed soils.

A correlation between the robustness of rhizomes and the depth of their occurrence has already been recognised by Salisbury ((11), p. 365).

The dry weights of tops and roots on examination yield the following results. In the first two cultures the averages of the dry weights of tops are given, but in cultures III and IV the dry weights of single shoots only are given.

In culture I the dry weight of shoots for compressed soils is 0·395 gm., for intermediate soils 0·478 gm., and for loose soils 0·478 gm.; in culture II for compressed soils 0·382 gm., for intermediate soils 0·392 gm., for loose soils 0·407 gm.; and the dry weights of shoots are 0·54, 0·72 and 0·52 gm. for compressed soils, 0·51, 0·53 and 0·47 gm. for intermediate soils, and 0·55, 0·62 and 0·63 gm. for loose soils in cultures III and IV.

ROOTS   **TOPS**

Loose

Intermediate

Compressed

0   ·1   ·2   ·3   ·4   ·5   ·6   ·7   ·8
Dry weight in gm.
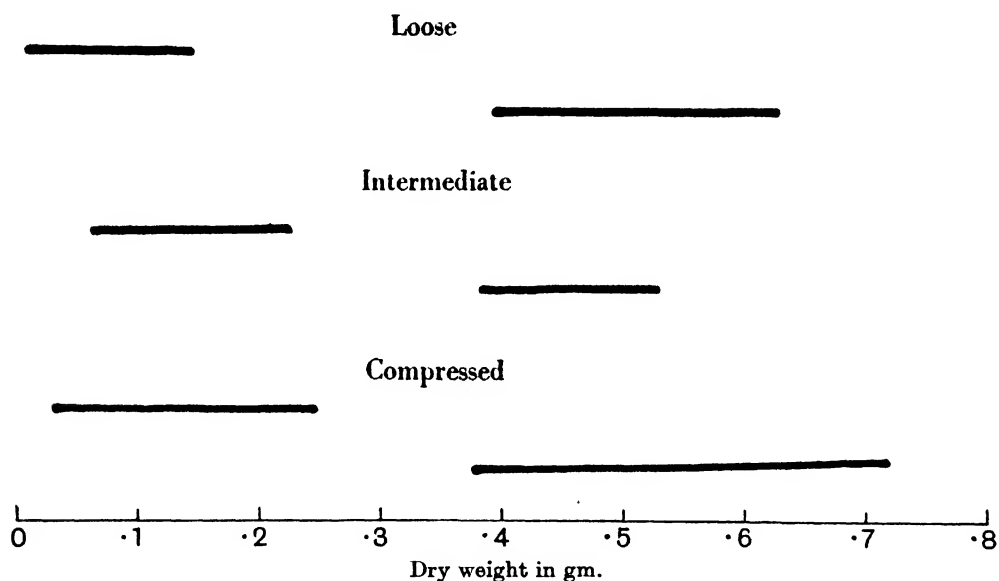
GRAPH 4. Dry weight of tops and roots (beans). Cultures I–IV. (Showing range.)

The mean dry weights of roots are:

	Compressed soil gm.	Intermediate soil gm.	Loose soil gm.
Culture II	0·127	0·175	0·065
Culture III	0·20	0·20	0·15
Culture IV	0·11	0·085	0·105

The range of dry weights of tops is for compressed soils 0·382–0·72 gm., for intermediate soils 0·392–0·53 gm., and for loose soils 0·407–0·63 gm. The range of dry weights of roots for compressed soils is 0·04–0·25 gm., for intermediate soils is 0·07–0·23 gm. and for loose soils is 0·02–0·15 gm., and these have been shown in Graph 4. So far as these meagre data can be relied on they indicate no significant differences in the dry weights of tops of plants grown under the three sets of conditions, but the dry weights of roots would

appear to tend to increase with increasing compression. Thus though the root systems in the compressed soil occupy a smaller volume of soil this volume is more completely exploited.

In the culture experiments summarised above, the soil as we have seen was compressed in pots artificially to vary the density of the soil by bringing together the individual particles. In doing so we were not only increasing the density but also reducing the pore space enclosed by the particles and consequently the amount of water, air and oxygen available for roots. Not only are we varying the amount of water and air in the pore space, but the rate of diffusion of CO_2 from the soil into the air and of oxygen from the atmosphere to the soil will also be effected (Buckingham (**2**)).

Diffusion depends mainly on the total pore space and not to any great extent on the dimensions of the individual pores. This fact will help us in settling the question of differential aeration in our pots, as all the direct evidence which could have been forthcoming by waterlogging the cultures to equalise aeration with *Vicia faba* proved negative, since all the cultures failed completely. Waterlogged cultures were carried out with *Phaseolus multiflorus*, *Helianthus annuus* and *Vicia faba*, but all failed. In neither case did the seeds germinate nor the germinated seeds proceed further when transferred to water-logged pots.

(*f*) Culture experiments—oats.

Another series of culture experiments was started with *Avena sativa*. Oats, as Cannon (**3**) points out, are markedly tolerant of bad aeration. The soil as before was used in three grades, i.e. compressed, intermediate and loose, and the pots were exposed to similar conditions of light and temperature. As the percentage of germinating seeds is rather low in grasses, a number of seeds were put in each pot, and when the seeds germinated, the plants were thinned out so that equal numbers remained in each pot.

Two series of culture experiments were carried out with oats, and a third series was started in which the soil was maintained in waterlogged condition, all other conditions being the same. In due course the plants were ready for further examination and morphological studies.

(i) *Ordinary cultures.*

On cutting, the mean heights of tops were found to be 52·5 cm. for loose soils, 51·8 cm. for intermediate soils, and 41·2 cm. for compressed soils (culture I). The mean heights of tops in culture II were 22·3 cm. for loose soils, 19·3 cm. for intermediate soils, and 18·9 cm. for compressed soils.

The mean length of roots in cultures I and II were 15·3 and 11·5 cm. for loose soils, 15·7 and 7·1 cm. for intermediate soils, and 9·9 and 6·9 cm. for compressed soils. The mean diameter of roots being 3·4 div. for loose soils (5·8 div. = 1 mm.), 3·8 div. for intermediate soils, and 4·4 div. for compressed soils

(culture I). Very similar results were obtained from culture II. The diameter or thickness of roots clearly suggests that the roots were thicker generally in compressed soils as compared with loose soils.

The mean dry weights of tops were 0·350 gm. for loose soils, 0·350 gm. for intermediate soils, and 0·218 gm. for compressed soils (culture I), 0·018 gm. for loose soils, 0·012 gm. for intermediate soils, and 0·016 gm. for compressed soils (culture II). These dry weights indicate that the plants in all the three sets were almost equally conditioned.

Finally the mean dry weight of roots were 0·008 gm. for loose soils, 0·011 gm. for intermediate soils, and 0·012 gm. for compressed soils. A tendency in the dry weights of roots to rise from loose soil to compressed soil is very clear.

(ii) *Waterlogged cultures.*

Now we will consider the waterlogged cultures in which the differential aeration was eliminated and only the density of the soil allowed to act.

The mean height of tops was 20·6 cm. for compressed soils, 31·9 cm. for intermediate soils, and 20·85 cm. for loose soils. The same relation is true of the root systems, the means in this case being 3·35 cm. for compressed soils, 4·15 cm. for intermediate soils, and 3·86 cm. for loose soils. Finally, the mean dry weight of tops was 0·05 gm. for compressed soils, 0·122 gm. for intermediate soils, and 0·08 gm. for loose soils, and for the roots 0·006 gm. for compressed soils, 0·01 gm. for intermediate soils, and 0·01 gm. for loose soils.

If these results are compared with those obtained in cultures which were not waterlogged, it will be seen that the results conform in both cases very strikingly. The results of culture I, already quoted, are reproduced below.

Oats, culture I, not waterlogged.

State of soil	Length of tops cm.	Length of roots cm.	Dry weight of tops
Loose	52·5	15·3	0·350
Intermediate	51·8	15·7	0·35
Compressed	41·2	9·9	0·218

In cultures I and II the oats were subjected to the influence of two varying factors in the soil, the density of the soil and unequal aeration. In the waterlogged culture the second factor was equalised, and only the density of soil was variable, still the results are similar in the normal culture I and in the waterlogged culture. We therefore appear justified in attributing to the density of soil alone the results obtained above.

The mechanical resistance to be overcome by the roots in penetrating the denser soil involves the expenditure of increased energy which is reflected in the smaller root system. This results in a reduced absorbing surface and a smaller volume of soil exploited, thus reacting on the growth of the plant which, as we find, is less in the compressed soils. The diminished growth in the
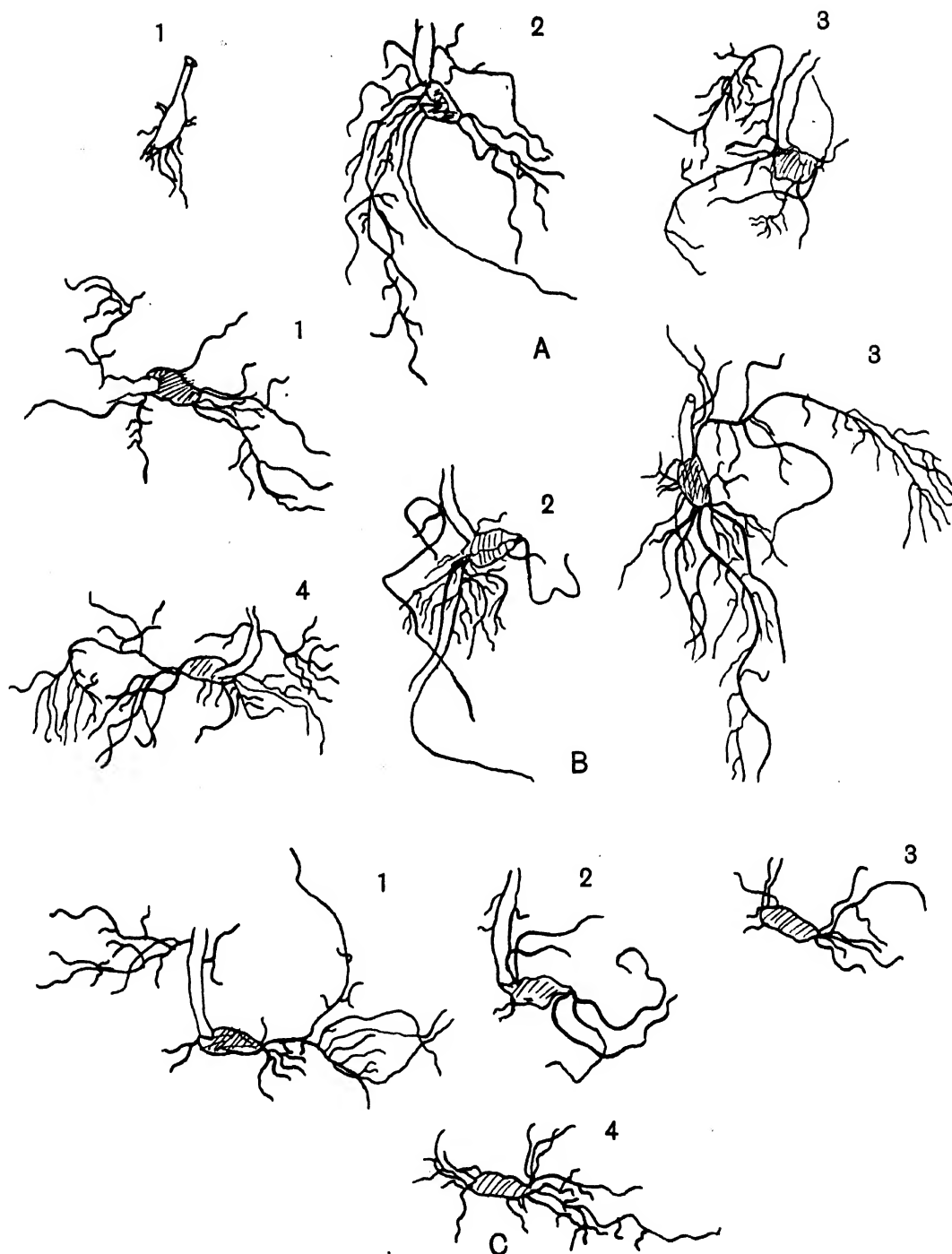
FIG. 1. Water logged oats. Root systems. A, loose soil. B, intermediate soil.
C, compressed soil. (About ½ natural size.)

loose soil which is seen alike in the normal and waterlogged cultures, though more marked in the latter, is perhaps to be attributed to a less intimate contact between root and soil particles and is indicative of an optimum degree of packing of the soil particles when there is a balance between the adverse mechanical resistance of increasing density and beneficial effects of intimate contact.

Table VIII. *Waterlogged cultures (oats)*.

	Height of tops			Length of roots	
Compressed soil cm.	Intermediate soil cm.	Loose soil cm.	Compressed soil cm.	Intermediate soil cm.	Loose soil cm.
23·0	34·0	33·5	4·2	5·8	5·3
22·5	33·7	25·0	4·2	5·6	4·2
18·8	30·0	14·7	2·8	2·9	1·5
18·2	29·8	10·2	2·2	2·3	—
Mean 20·6	31·9	20·85	3·35	4·15	3·66

	Dry weight of tops			Dry weight of roots	
Compressed soil gm.	Intermediate soil gm.	Loose soil gm.	Compressed soil gm.	Intermediate soil gm.	Loose soil gm.
0·07	0·14	0·12	0·01	0·01	0·01
0·05	0·14	0·09	0·00	0·01	0·01
0·05	0·11	0·06	0·01	0·01	—
0·03	0·10	0·05	—	—	—
Mean 0·05	0·122	0·08	0·006	0·01	0·01

Having studied the cultures both with *Vicia faba* and *Avena sativa*, we are in a much better position now to discuss the real importance of the mechanical factor of the soil as determined by its texture on growth of plants. Waterlogged cultures having failed completely in the case of beans the constantly varying factor—the differential aeration—could not be eliminated, and we are faced with the argument as to whether the results obtained might not be the effect of the differential aeration. In fact some results obtained in my experiments point very strongly in the direction of differential aeration as playing an important part. Superficial disposition and shorter lengths of the root systems, observed in the denser soils, are common to both defective aeration and increased resistance.

It is generally understood that increased resistance from the soil involving a reduced pore space means checking of proper diffusion of gases and thus causing bad aeration in the soil. It has been pointed out previously that diffusion of gases does not merely depend upon the dimensions of the individual pores.

As the waterlogged cultures with oats showed similar morphological differences to those in the normal cultures, the effects may be attributed to the resistance of the soil. With respect to the bean cultures, neither in the rate of growth, nor in the height of shoots, nor indeed in the area of the assimilatory organs do we find any significant differences in the plants growing in the three

grades of the same soil. No unhealthy symptoms are exhibited by plants in any of the soils, and they keep pace remarkably with one another in the three soils. Differential aeration in the pots might be expected to bring about differences in all or any of the factors considered above. The dry weights, indicating as they do the metabolic activities of the plants during their life times, show us that there has been no lowering of those activities in any of the plants by compressing the soils mechanically and thus causing differential aeration. From such data as we have it would appear that plants in the different soils were equally conditioned as regards metabolic activities.

The underground organs, which would be the first to be affected by differential aeration, provide us with further evidence for the relative unimportance of this factor in producing the differences noted. The roots are superficial and generally thicker, with laterals arising from the main root just below the beginning of the shoot in the denser soils and not arranged in regular order on either side of the long main root as in loose soil. The length of the main root is of particular interest; whereas, in loose soils, it can attain a length of 42 cm., in denser soils it can grow only 2 or 3 cm. The superficial character of the root system may be correlated equally with mechanical resistance and diminished aeration, but the diminished length and increased thickness are features unlikely to be influenced by the condition of aeration, and indeed an extensive root system might tend to offset the effect of bad aeration.

The dry weights of roots indicate that though they are faced with the difficulty of pushing their way through the soil, their activities are not affected to any marked degree; on the contrary, they exploit the soil they are in contact with more completely, showing a better dry weight in compressed soils. A tendency towards increase in dry weight in the roots can hardly be expected in badly aerated soils. Development of root hairs and lack of any aeration tissue in the root in compressed soil further supply evidence against bad aeration.

(g) Field observations.

In order to ascertain how far the preceding laboratory results correspond with conditions in nature field observations were made in a number of localities. *Mercurialis perennis* was selected for this purpose, as it grows on a variety of soils. The length and thickness of the internodes and the density of the soil at the level at which the rhizomes grew were determined. It will be seen from Table IX, that the relation between these features is maintained to a fair degree. The longest and thinnest internodes are met with in soils which have the highest surface penetrability, the shortest and the thickest internodes were found in clay which had the lowest surface penetrability.

The correlation of the robustness of rhizomes with the depth of their occurrence as recognised by Salisbury (9), and my results with beans and oats

and *M. perennis* rhizomes found in soils of different texture, leave no doubt as to the importance of the texture of the soil on the underground organs. The modification of the underground organs in response to the texture of the soil has obvious advantages for the plant in the way of overcoming the resistance.

Table IX. *Relationship between internodes of* Mercurialis perennis *and surface penetrability.*

Locality and soil	Mean surface penetrability	Length of internodes in cm.			Thickness of internodes in mm.		
		Min.	Mean	Max.	Min.	Mean	Max.
Bricket Wood (clay)	3·07	1·7	6·17	14·0	1·2	2·05	4·2
Oxted (clay)	4·03	0·9	5·05	17·2	1·0	1·90	3·0
Orpington (clay with sand)	4·2	3·5	7·8	18·4	1·5	2·0	3·0
Woldingham II (chalk)	4·8	4·8	10·5	24·0	1·0	1·8	2·8
Woldingham I (chalk)	6·06	3·2	8·6	21·5	1·3	2·0	3·0

Lastly, it was attempted to get some idea of penetrability of soils in nature at different depths (Tables X and XI), and to find out any relation between moisture content in the soil and penetrability (Table X). Special tins were required to take out a profile of soil from the field. The tins used were about double the size of the ordinary 2-oz. tobacco tins, pierced with three or four rows of holes, big enough to allow the penetrability apparatus rod free play. Each row contained five holes at equal distances. These tins were pressed into the field, and then taken out. It will be seen that the soil was supported on all sides as in nature, and penetrability determined, without in the least disturbing the soil, by placing the tins in a horizontal position under the apparatus.

In Tables X and XI are shown the results from three different localities, i.e. clay from Oxted, chalk from Woldingham and clay with sand from Orpington. It is very clear from both the tables that the penetrabilities decrease. as the density increases, accompanying the increasing depth and varies directly with the moisture content of the soil. When we consider the penetrability with natural water content (Woldingham set I) we find that it drops rapidly from the surface to the sub-surface, i.e. 6·06 to 4·14 and then for subsequent layers falls gradually, i.e. 4·14 to 3·0 and 3·0 to 2·9. The same is true of other localities. But in the Orpington samples this rule is departed from, as the carpet of humus was not of any noticeable thickness and the soil was remarkably homogeneous as compared with the calcareous soils where lumps of chalk and stones were frequently met with. The importance of organic material and moisture content of the field cannot be therefore over-emphasised in being instrumental in affecting penetrability. In the Orpington samples the effect of the sand with the clay is also very apparent. It shows a low maximum water capacity of 45·7 per cent. as compared with pure clay of 59·5 per cent. and chalk of 74·0 per cent. on the one hand and exhibits

an increased penetrability as compared with these soils on the other (Table X).

Table X. *Penetrability.*

| | | Chalk, Woldingham | | | | | | | Clay with sand, Orpington | | |
| | Clay, Oxted | | Set I | | | Set II | | | | | |
Depth cm.	46·3 %	59·5 %	41·1 %	52·3 %	74·0 %	33·5 %	45·6 %	69·8 %	23·3 %	32·1 %	45·7 %
1·5	2·8	4·2	4·1	6·06	—	3·0	4·8	6·0	2·6	4·2	7·9
3·0	1·3	2·8	3·2	4·14	6·0	2·5	3·2	4·3	1·9	3·4	5·5
5·0	0·9	2·1	2·1	3·00	5·7	1·4	2·5	3·2	1·0	2·6	5·6
6·5	—	2·2	1·4	2·90	4·9	—	2·1	2·5	0·4	—	4·4

Table XI. *Relation of penetrability to depth of soil and moisture content.*

Bricket Wood, Radlett.

| | Sample I | | Sample II a | | Sample II b | | Sample III | | Sample IV | | Sample V (chalk) | |
Depth cm.	40·9 %	49·4 %	23·3 %	52·1 %	43·0 %	62·9 %	44·5 %	50·6 %	45·3 %	48·3 %	40·9 %	63·7 %
1–1·5	2·9	2·3	4·3	8·0	4·1	3·5	2·8	3·3	2·4	2·3	4·4	4·6
3–3·5	3·1	4·3	1·7	3·9	1·2	2·7	1·7	3·1	1·0	2·8	3·0	4·0
5–5·5	2·9	3·9	0·55	2·8	1·0	2·3	1·0	2·5	0·55	1·8	2·9	5·0
7–7·5	2·1	2·3	0·6	—	—	—	1·5	1·9	0·8	2·0	3·3	7·5
9·0	1·6	1·7	—	—	—	—	1·0	1·6	—	4·4	—	—

Spark Estate, Oxted.

| | Sample I | Sample II | | Sample III | Sample IV | | Sample V | | Sample VI |
Depth cm.	55·1 %	53·7 %	66·5 %	59·9 %	41·08 %	55·3 %	44·3 %	58·8 %	61·8 %
1–1·5	4·1	2·7 ·	3·7	5·7	2·2	3·7	3·6	3·9	4·1
3–3·5	2·5	1·6	2·9	3·2	1·0	1·7	1·3	3·6	2·4
5–5·5	2·0	1·4	2·2	1·9	0·8	1·9	0·5	2·4	1·9
7–7·5	2·4	1·1	2·5	1·9	—	—	—	—	1·9

From the two sets collected from Woldingham the first gives an average field water content of 52·3 per cent. with surface penetrability of 6·06, while the second gives an average field water content of 45·6 per cent. with 4·8 as surface penetrability. The first set was collected after a shower, and it will be seen how the penetrability is affected by moisture, dropping from 6·06 to 4·8 when the natural field water content changed from 52·3 to 45·6 per cent.

No clearer relationship between penetrability and water content can be found than in the samples from Woldingham and Orpington. Set I from Woldingham shows that when the field water content of 52·3 per cent. is lowered to 41·1 per cent. the surface penetrability falls from 6·06 to 4·1, and when the water content was raised to 74·0 per cent. the soil had become so soft that the rod of the penetrability apparatus went right through.

Set II gives the same results: when the field water content of 45·6 per cent. is lowered to 33·5 per cent. the penetrability is lowered from 4·8 to 3·0 and when the water content is raised to 69·8 per cent. the penetrability increases from 4·8 to 6·0.

Orpington samples finally show that on lowering the field water content 32·1 to 23·3 per cent. the penetrability falls from 4·2 to 2·6, and on raising the water content to 45·7 per cent. the penetrability rises to 7·9.

(h) SUMMARY.

The physical properties of soil under artificial compression have been studied. Quantitative determinations are furnished of the effect of artificial compression on water capacity, resistance to flow of water, absorption of water, pore space and penetrability.

Culture experiments with beans and oats have been carried out with a view to finding out the direct effect of the density of the soil on growth of these species. The results in general show that with regard to height of tops and area of assimilatory organs the plants in both cases are more or less equally conditioned, i.e. density of soil has little effect on them, but as regards the underground organs they are markedly modified, resulting in smaller and stronger root systems in denser soils. While the dry weight of tops shows no marked differences, the dry weight of roots in denser soils tends to indicate that though the root systems are smaller, the soil has been more completely exploited.

Experiments with waterlogged cultures in beans failed, but with oats similar results were obtained as with compressed soils without waterlogging; thus the differences observed between growth in compressed and uncompressed soils can be attributed to the soil texture, and not to the result of diminished aeration. Presence of root hairs and absence of any aerating tissue in the root are further evidence that no important part is played by differential aeration in this connection consequent on compressing the soil.

Lastly, an attempt has been made to evaluate the relation under natural cnoditions between the internodes of rhizomes of *Mercurialis perennis* and texture of the soil on which it grows. The results show that internodes in clay are smaller and thicker in comparison with those in chalk, where they are long and thin.

Data respecting the penetrability of the soil at successive levels in the natural plant communities have been obtained and the relation to water content determined. The penetrability in general tends to decrease with increase in density which usually accompanies increase in depth from the surface. The penetrability also varies directly with the moisture content.

The data submitted indicate that the mechanical properties of the soil as determined by its texture are of considerable importance as affecting plant growth.

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THE COMPOSITION OF THE SOILS USED IN THE POTTERNE TRANSPLANT EXPERIMENTS AND OF PORTIONS OF *CENTAUREA* AND *SILENE* GROWN THEREON[1]

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THE soils used in the experiments were four in number, and may be briefly described as a sand and calcareous sand, a clay and a calcareous clay. For information as to their origin reference should be made to this JOURNAL, **18**, p. 353. The analyses refer to samples of the soils before the plants were grown on them.

The two sands were not precisely similar in their physical composition, while the high percentage of calcium carbonate in the calcareous clay makes any direct comparison between them difficult. The percentage figures of the two calcareous soils are therefore also given after exclusion of the calcium carbonate (columns II *a* and IV *a*).

The figures for their physical composition, as shown by their mechanical analyses, are given below:

| | Sand | Calcareous sand | | Clay | Calcareous clay | | Potterne soil |
	I	II	II*a*	III	IV	IV*a*	V
Coarse sand	80·6	69·7	77·0	2·8	0·8	1·7	21·8
Fine sand	8·3	9·2	10·0	43·2	16·1	33·0	55·7
Silt	3·9	4·2	4·6	19·5	6·7	13·3	5·1
Clay	6·4	5·2	5·7	29·9	16·5	34·5	12·7
Loss in solution	0·5	2·7	—	2·0	60·2	—	1·6
Organic matter (loss on ignition)	2·6	1·5	—	3·5	6·4	—	3·4
Hygroscopic water	0·6	0·6	—	4·7	2·9	—	2·7
CaCO₃	Nil	9·5	—	0·4	52·2	—	0·2

The figures in columns II*a* and IV*a* are percentages of the different physical components of soils II and IV, calculated after omission of CaCO₃ so as to give a more direct comparison with the physical composition of the other soils.

It will be seen from these figures that the two sands were fairly similar in texture, and the texture of the clays is also fairly comparable when the percentages are calculated after exclusion of the calcium carbonate. Similar figures for the garden soil at Potterne are also given. The chemical analysis which has been carried out so far has been with the object of obtaining some information on the status of the four soils as regards plant nutrients, and for this purpose the older methods of solution in hydrochloric acid and citric acid have been followed.

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[1] Addendum to the Report printed on pp. 268–93 of this issue.

It is proposed to augment this in later work by determination of the exchangeable calcium, and other bases contained in the soil.

	I	II	III	IV	V
Nitrogen	0·04	0·02	0·12	0·16	0·13
P_2O_5 sol. in HCl	0·12	0·15	0·04	0·16	0·07
P_2O_5 sol. in 1 % citric acid	0·002	0·007	0·012	—	0·025
K_2O sol. in HCl	0·09	0·15	0·55	0·15	0·63
K_2O sol. in 1 % citric acid	0·007	0·034	0·037	—	0·021

The figures shown above are very much what would be expected from the physical texture of the soil. The amounts of nitrogen increase with the increase in fineness of the soil, and are in no way abnormal.

The phosphorus content of the sands is low, but not abnormally so, though the amounts soluble in citric acid are very low in these two cases. In the two clays the phosphorus content of No. III is low, while that of No. IV is normal and the citric acid-soluble phosphate of No. III is very high. Owing to the high percentage of calcium carbonate in No. IV, it was not possible to use this method.

The potash content of Nos. I and II is normal, but the solubility of the potash in No. II is high, in No. III the total potash is not high but its solubility is, while No. IV shows a very low potash content due no doubt again to its high percentage of calcium carbonate. Its solubility was not determined for the reason already given. The Potterne soil shows a normal content of these plant nutrients with the high solubility usually associated with land in a good state of cultivation.

The reaction of these soils was determined by an electrometric method, and gave the following results:

	I	II	III	IV	V
pH	7·3	8·3	7·4	8·6	6·6

These were determined in the fresh moist soil. It will be observed that none of this soil gives an acid soil water suspension except the Potterne garden soil.

In view of the work which has been done on the change in H^+ ion content of soil water suspensions, before and after drying parallel determinations were made in these soils after air drying.

	I	II	III	IV	V
pH	6·5	7·9	7·1	8·1	5·1

The figures are interesting, but are not capable of any exact interpretation at the present time. It is perhaps surprising that in soils so well buffered as Nos. II and IV, so large a change should take place. In view of these changes it is considered that it is the range of pH which should be taken as a soil character rather than the pH figure in either the wet or the dry state.

It was not expected to get any more figures which would be of interest from an examination of the soil until the experiment had been running for a longer time.

In two successive years, analyses were made of some of the plant material grown. *Centaurea nemoralis* was chosen for this part of the investigation because of the large amount available. In the first year only the leaves were examined, and in the second year leaves of *Centaurea* and roots of *Silene vulgaris*.

Determination of nitrogen, of total ash content and of calcium, phosphorus, and potash in the ash—the figures are given below.

First collecting year.
Centaurea leaves (9. x. 1930).

	I	II	III	IV	V
Nitrogen	2·3	2·2	2·2	2·1	2·3
Total ash	14·1	11·2	12·8	12·6	17·5
Ca % in ash	10·6	10·7	10·5	13·6	8·2
P_2O_5 % in ash	5·1	7·5	7·1	6·9	5·4
K_2O % in ash	18·7	27·9	26·0	28·2	19·8

Second collecting year.
Centaurea leaves (28. x. 1931).

	I	II	III	IV	V
Nitrogen	2·3	1·7	2·3	2·0	2·4
Total ash	12·8	10·8	12·2	12·5	16·3
Ca % in ash	6·5	14·5	13·5	16·5	11·7
P_2O_5 % in ash	7·5	8·1	8·5	7·4	8·6
K_2O % in ash	26·0	27·0	30·0	28·9	28·1

Silene roots (28. i. 1932).

	I	II	III	IV	V
Nitrogen	1·9	1·4	2·4	2·0	2·5
Ca % in ash	12·5	15·8	9·8	19·5	11·4
P_2O_5 % in ash	8·9	12·5	9·2	11·3	11·0
K_2O % in ash	21·4	22·6	16·9	21·4	18·2

The results obtained from this investigation show the extent to which the composition of the plant is affected by its root environment.

In all the leaves, except those grown on soil II in the second series, the nitrogen content of the whole series is practically constant and independent of the environment, indicating that, however unsuitable the environment might be, the plant required to manufacture a similar quantity of protein.

The total ash figures are high, but there is no doubt that there was in some cases considerable contamination with soil from which it was impossible to free the material altogether. It is, however, perhaps significant that in both series the highest ash content is shown by the Potterne soil.

The phosphorus content is lowest in I and IV in both seasons, which is probably what would be expected from the low soluble phosphorus content of soil No. I and the high calcium carbonate content of soil No. IV.

The calcium figures show comparatively little variation in the first year, though even here the figures are lower for I and III than they are for II and IV. In the second year the differences are more marked and soil No. I, due to its

great porosity and the leaching effect of the annual rainfall, is causing a marked calcium deficiency which is not seen in any of the others. Soil No. III, owing to its finer texture and to the much smaller amount of leaching that can take place, still maintains its calcium content very little below that of the plants from the calcareous soil.

Potash is not noticeably deficient, except in soil No. I, which deficiency is reflected in the leaves in the first year, though not subsequently.

The figures for the roots of *Silene* are not easy to interpret; the nitrogen content is low in the case of the two sands and high in the case of the other two experimental soils and the Potterne soil.

The calcium content is low in the soils which contain little of it, and the phosphorus is also low in the same soils. The potash figures vary considerably for no apparent reason. It would be desirable to repeat these analyses another season, if possible with another plant.

The general conclusion which may be drawn from a consideration of the composition of the soil and of the plants is that the soil environment not only affects the character of the growing plant but also considerably influences its composition. It is certain that a plant growing in a soil poor in certain constituents is only able to obtain a small quantity of them, and it may be that it is this lack of a specific substance which causes the change in form and general appearance. This aspect of the problem must be borne in mind as well as the more obvious physical characters of the soil environment which affect water and air supply and consequently root development.

The analyses quoted were carried out by Mr F. Carter, assistant in the Soil Science Laboratory, Oxford, to whom my thanks are due.

REVIEWS

THE WATER RELATIONS OF PLANTS

DER WASSERZUSTAND (HYDRATUR) UND SEINE BEDEUTUNG FÜR DAS LEBEN DER PFLANZE.

VON H. WALTER (*Stuttgart*).

Die Untersuchungen der letzten Jahre haben Verfasser zu einer neuen Anschauung in bezug auf den Wasserhaushalt der Pflanze geführt. Eine Zusammenfassung ist in der Abhandlung "Die Hydratur der Pflanze und ihre physiologisch-ökologische Bedeutung[1]" gegeben worden; um aber die der Betrachtung zugrunde liegenden Gesichtspunkte besser verstehen zu können, sei hier eine kurze historische Entwicklung der Gedankengänge vorausgeschickt.

Bei Plasmolyseversuchen mit Algen konnte Verfasser im Jahre 1923 feststellen, dass das Volumen des Plasmas nicht konstant bleibt, sondern dass es um so mehr abnimmt, je höher die Konzentration der angrenzenden Lösung ist. Durch die osmotische Saugkraft der Lösung wird also eine Entquellung des Plasmas hervorgerufen. Auf Grund von exakten Messungen konnte gefunden werden, dass *die Quellungskurve des lebenden Plasmas in Abhängigkeit von der relativen Dampfspannung denselben Verlauf zeigt wie diejenigen toter Quellkörper* (Gelatine, Kasein, Nuklein, Stärke). Die Quellungsgesetze haben also allgemeine Gültigkeit auch für die lebende Substanz. Im Gegensatz zu der weitverbreiteten Anschauung, dass das Quellungswasser durch den Quellkörper sehr fest gebunden ist, zeigt es sich, dass der grösste Teil des Wassers sehr leicht abgegeben wird und nur der Rest sich erst durch äusserst hohe Saugkräfte entfernen lässt.

Wenn aber der Quellungszustand des Plasmas stark variabel ist, so ist anzunehmen, dass dadurch auch alle Lebensvorgänge, die sich doch im Plasma abspielen, davon in starkem Masse beeinflusst werden. Das zu prüfen, war die nächste Aufgabe. Als Versuchsobjekte dienten 1924 hauptsächlich Schimmelpilze, die man leicht in einer Kammer auf Substrat von bestimmter relativer Dampfspannung kultivieren kann. Durch Veränderung der relativen Dampfspannung in der Kammer kann man auch den Plasmaquellungszustand in den Zellen ändern. Es zeigte sich, dass die Wachstumsvorgänge in stärkstem Masse von der Plasmaquellung abhängen, obgleich den Pflanzen absolut gleiche Wassermengen zum Wachstum zur Verfügung standen. Gleichzeitig konnte festgestellt werden, dass für jede Art eine untere Grenze der Plasmaquellung vorhanden ist, bei der die Wachstumsvorgänge zum Stillstand kommen; sie entspricht einer ganz bestimmten relativen Dampfspannung. Die absolute Grenze für aktives Leben überhaupt ist bisher bei einer relativen Dampfspannung von 85 % gefunden worden.

Versucht man nun diese für Mikroorganismen gültigen Ergebnisse auf die höhere Pflanze zu übertragen, so stösst man gleich auf grösste Schwierigkeiten. Bei den Mikroorganismen hat der durch die relative Dampfspannung gekennzeichnete Wasserzustand des Aussenmediums einen unmittelbaren Einfluss auf den Wasserzustand der Zelle—auf die Plasmaquellung. Bei

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[1] Ein mit W. O. J. gezeichnetes Referat darüber ist im letzten Heft dieser Zeitschrift erschienen. Leider scheint Referent nicht in genügendem Masse die deutsche Sprache zu beherrschen und die einschlägige physiologische Literatur überhaupt nicht zu kennen. Dessungeachtet ist das Referat in einem so anmassendem Tone geschrieben, dass wir es ablehnen müssen, auf die gänzlich haltlosen Einwände zu antworten, und dem Referenten zunächst ein gründliches Studium des Problems empfehlen.

der höheren Pflanze ist das nicht der Fall. Sie wurzelt in einem Medium mit stets sehr hoher relativer Dampfspannung[1], während die oberirdischen Teile oft von einer extrem trockenen Luft umgeben sind. Aber diese hat keinen unmittelbaren Einfluss auf den Wasserzustand der Pflanzenzellen, denn die höhere Pflanze besitzt ja in ihrem Inneren eine eigene Atmosphäre und die Plasmaquellung wird unmittelbar nur vom Wasserzustand der letzteren beeinflusst.

Sollen wir nun, um die Wasserverhältnisse der Pflanze richtig beurteilen zu können, die relative Dampfspannung in dem Interzellularensystem bestimmen oder was technisch leichter und im Prinzip dasselbe ist—die Saugkraft der Zelle nach Ursprung? Will man die Fähigkeit der Zelle, Wasser aufzunehmen, messen, so ist die Saugkraft der Zelle die alleinrichtige Bezugsgrösse. Wir wollen aber nicht die Wasserverschiebung von Zelle zu Zelle untersuchen, wir wollen vielmehr den Wasserzustand der lebenden Substanz—die Plasmaquellung— bestimmen, und für diese ist die Saugkraft der Zelle nicht das richtige Mass, vielmehr wird sie, wie wir anfangs sahen, durch die osmotische Konzentration der Lösung bestimmt, an welche das Plasma grenzt, d.h. durch die Konzentration des Zellsaftes.

Diese mehr theoretischen Erörterungen führten schon 1925 und 1926 bei der zusammenfassenden Behandlung des Wasserhaushaltes der Pflanze und des Xerophytenproblems zu dem Ergebnis, dass dem osmotischen Wert des Zellsaftes eine zentrale Stellung für die Beurteilung der Wasserverhältnisse der Pflanze zukommt. Gleichzeitig kann der osmotische Wert uns auch als Indikator für die Wasserbilanz der Pflanze dienen, während Wasseraufnahme, Wasserleitung und Transpiration jede für sich nur Teilvorgänge im Wasserhaushalt der Pflanze bilden und uns keinen allgemeinen Begriff von den Wasserverhältnissen der Pflanze zu vermitteln vermögen.

Gewiss sind osmotische Untersuchungen schon seit langem ausgeführt worden und namentlich von amerikanischer Seite wurde auch neuerdings immer wieder auf die Bedeutung des osmotischen Wertes hingewiesen. Aber stets sah man die Hauptrolle der osmotischen Kräfte darin, der Pflanze die Fähigkeit zu verleihen, Wasser aus dem Boden aufzunehmen. Eine Erhöhung der Zellsaftkonzentration wurde deshalb als eine zweckmässige Anpassung an trockene Standorte gedeutet und sollte für die Pflanze nützlich sein. Wir stehen dagegen auf einem prinzipiell anderen Standpunkt. Die Erhöhung der Zellsaftkonzentration an trockenen Standorten ist nur die Folge einer unausgeglichenen Bilanz, wenn die Pflanze mehr Wasser durch Transpiration verliert, als sie aus dem Boden aufnehmen und den Blättern zuführen kann. Und diese Erhöhung kann nicht als nützliche Anpassung betrachtet werden, sondern sie ist eher schädlich; denn sie muss ja unmittelbar zu einer Entquellung des Plasmas führen. Die Folge davon ist wiederum, dass der Ablauf aller physiologischen Vorgänge gestört wird, das Wachstum hört auf, die CO_2-Assimilation wird gehemmt. Geht die Entquellung noch weiter, so tritt schliesslich der Tod ein.

Es galt nun die experimentellen Grundlagen als Beweis für die Richtigkeit dieser Anschauungen zu schaffen. Die Versuche konnten nicht im Laboratorium ausgeführt werden, vielmehr diente als solches die Natur selbst und damit war der Übergang von rein physiologischen zu ökologischen Untersuchungen gegeben. Nicht schematische Bestimmungen von Mittelwerten, nicht die gedankenlose Anhäufung von vielen Zahlenwerten konnten hier zum Ziele führen, sondern nur vergleichende Untersuchungen des osmotischen Wertes derselben Pflanzenarten an möglichst vielen verschiedenen Standorten, sowie möglichst kurzfristige Probenentnahmen am selben Standort bei verschiedenen Witterungsverhältnissen. Die Zusammenhänge klar herauszuarbeiten, gelang es aber erst, als die Verhältnisse in den verschiedenen Klimazonen von der subtropischen Wüste bis zur oberen Grenze der Vegetation im Hochgebirge untersucht worden waren.

Es zeigte sich erstens, dass wir die Pflanze selbst als besten Indikator für die Wasserverhältnisse an verschiedenen Standorten oder am selben Standort zu verschiedenen

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[1] Selbst Böden, deren Wassergehalt dem Welkungskoeffizienten entspricht, besitzen eine relative Dampfspannung von über 99 %.

Jahreszeiten heranziehen können, wenn wir ihren osmotischen Wert bestimmen. Zweitens sind die einzelnen Pflanzen sehr verschieden empfindlich für Veränderungen in der Aussenwelt: ein trockener Standort ist durchaus nicht für alle Arten gleich trocken; während bei den einen Arten der osmotische Wert sich bereits sehr stark erhöht, reagieren die anderen überhaupt noch nicht und zeigen ein sehr grosses osmotisches Beharrungsvermögen. Ebenso verschieden sind die Grenzwerte, bei denen die Pflanzen geschädigt werden. Arten feuchter Standorte vertragen eine Erhöhung des osmotischen Wertes fast gar nicht. Arten trockener Standorte können zuweilen unter günstigen Wasserverhältnissen einen osmotischen Wert besitzen, der nicht wesentlich höher ist als bei Hygrophyten; sie vertragen aber bei Trokkenheit ganz enorme Steigerungen, ohne geschädigt zu werden. Sehr klare Beziehungen ergeben sich zwischen Wachstumsintensität und osmotischem Wert, zwischen der morphologischen Ausbildung und dem Wasserzustand, und es scheinen auch Beziehungen zur Blühfähigkeit zu bestehen; doch muss diese Frage erst noch genauer nachgeprüft werden.

Wir sehen also, es kommt in der Wasserökologie nicht darauf an, was für Wassermengen der Pflanze zur Verfügung stehen oder sie durchströmen; nicht die Transpirationsintensität oder die Wasseraufnahme sind direkt von Bedeutung, sondern nur der Wasserzustand der Pflanze, als dessen Mass uns die Konzentration des Zellsaftes dienen kann und die wir entweder in Atmosphären oder in Prozenten der relativen Dampfspannung ausdrücken. Um diese Tatsache zu betonen, wurde für den Wasserzustand in der letzten Zusammenfassung (1931) die Bezeichnung "Hydratur" vorgeschlagen, als deren Mass wir die relative Dampfspannung benutzen. Die Hydratur erreicht also ihr Maximum bei einer relativen Dampfspannung gleich 100, wenn wir z.B. reines Wasser vor uns haben, und sie ist um so stärker herabgesetzt, je konzentrierter eine Lösung, je höher also der osmotische Wert (in Atmosphären ausgedrückt) ist.

Um die Gedankengänge etwas anschaulicher zu machen, wiesen wir auf eine gewisse Analogie mit den Wärmeverhältnissen hin, die natürlich rein bildlich zu verstehen ist. Wir sind ja gewohnt, zwischen Wärmemenge (in Kalorien ausgedrückt) und Wärmezustand = Temperatur (in Graden Celsius ausgedrückt) zu unterscheiden. Und der Biologe weiss, dass bei seinen Untersuchungen meistens die Temperatur viel wichtiger ist als die Wärmemenge. Ähnlich ist es beim Wasser. Wir müssen streng zwischen Wassermenge (in Gramm ausgedrückt) und Wasserzustand = Hydratur (in Prozenten der relativen Dampfspannung gemessen) unterscheiden; und auch hier scheint es so zu sein, dass der Wasserzustand oder die Hydratur für biologische Vorgänge wichtiger ist, als die Bestimmung der Wassermenge.

Als Mass des Wasserzustandes können wir natürlich auch den osmotischen Wert, resp. Saugkraft in Atmosphären benutzen, und man wird sich die Frage vorlegen, ob es zweckmässig ist, eine neue Bezeichnung (Hydratur) überhaupt vorzuschlagen. Wenn wir es taten, so war dafür Folgendes massgebend. Man spricht immer von der Saugkraft als Eigenschaft eines bestimmten Körpers, z.B. einer Zelle, einer Lösung, des Bodens u.s.w. Uns lag es daran, zu betonen, dass das eigentlich nicht ganz richtig ist; denn es handelt sich nicht um die Eigenschaft der verschiedenen Körper (wie es etwa bei der Wärme der Fall ist), sondern stets um die Eigenschaft des in ihnen enthaltenen Wassers, um den Wasserzustand (Hydratur). Im übrigen ist es natürlich gleichgültig, welches Mass und welche Bezeichnung man bevorzugt, wenn man nur die Zusammenhänge richtig erfasst.

Wenn wir hier nur auf die Entwicklung der eigenen Gedankengänge eingingen und nur die eigenen Untersuchungen berücksichtigen, so soll damit keineswegs der Eindruck einer Überschätzung der eigenen Arbeit hervorgerufen werden. Es geschah nur aus Raummangel und um die Entwicklung der wichtigsten Gesichtspunkte klarer herauszuarbeiten. Denn es handelt sich um einen ersten Versuch, den Wasserhaushalt der Pflanzen einmal auch von einer anderen Seite her zu betrachten, als es gewöhnlich üblich ist.

In the *Journal of Ecology* for February Prof. Walter's monograph was criticised on the following grounds:

(1) The conception of "hydrature" is based on an imperfect analogy, involving a confusion between matter and energy.

(2) The idea that it seeks to express has already been better defined by Ursprung's "Saugkraft" (familiar in England as "suction force" and "suction pressure").

(3) It is hard to believe that equilibrium between the water content of the cytoplasm and the vacuole is so rapidly established as the method of measuring "hydrature" requires. No consideration is given to this difficulty.

(4) The ecological results given for particular habitats are often very scanty, and no information is supplied enabling one to estimate the reliability of the data.

It was also pointed out that there are rather numerous details open to criticism.

The author in his summary or "Autoreferat" written after reading these criticisms says that suction pressure is an objectionable term because it is applied to the absorbing body, e.g. soil, solutions, etc.: "hydrature" and temperature apply respectively to the water and heat contained by the body. Does Prof. Walter then never speak of the temperature of the air or soil, or the internal temperature of his plant? And why in this case does he speak of the "hydrature" of the soil and of protoplasm? It is, of course, the defects of the analogy upon which his terminology is based that leads him into this inconsistency.

In no other respect does the author make any attempt to meet the objections raised in the review.   W. O. JAMES.

DISTRIBUTION OF BRITISH PLANTS

Salisbury, E. J. *The East Anglian Flora: a study in comparative Plant Geography.* Reprinted from the *Transactions of the Norfolk and Norwich Naturalists' Society*, vol. XIII, pt. III, pp. 191–236, with eight plates, three text figs., and 106 maps. Price 5s. 1932.

In collecting data relating to the local distribution of plants and animals the Natural History Societies of this country have made no small contribution to our knowledge of the British flora and fauna, and the usefulness of such work needs to be recognised. Such information forms the basis for further lines of enquiry and in particular it becomes a matter of considerable interest to assemble the facts of geographical distribution so obtained in order to gain a wider view and visualise the problems which arise in whole rather than in part. This is what Prof. Salisbury has done for the East Anglian flora, the subject of his presidential address last year to the Norfolk and Norwich Naturalists' Society.

While the more noteworthy features of the flora of East Anglia are dealt with especially, the author extends the scope of his address beyond the limits of Norfolk itself, since he rightly insists that the significance of the plant population of Norfolk can only be appreciated in relation to that of Britain and the Continent as a whole. Before passing to the main subject of the address reference is made to some general considerations. Attention is drawn to the fact that species towards the limit of their geographical range show two extreme types of occurrence, (1) those which gradually become rarer as they approach their climatic limit, such as *Matthiola sinuata*, *Euphorbia hiberna* and *Ruscus aculeatus*, and (2) those which occur abundantly right up to their geographical limit, such as *Primula elatior*, *Erica ciliaris* and *E. vagans*. This mode of occurrence is held to depend mainly on the competition factor, the former type being characteristic of more open communities, the latter, frequently social species (this is probably very important), being members of advanced phases of succession, and characteristic of more closed plant communities. There are, however, numerous exceptions

to this general hypothesis and in addition to competition other factors must play a part in determining the degree of abundance of a species at the limit of its range.

The recent geological history of East Anglia is next considered and the vexed problem of the effect of the Pleistocene glaciation upon the general distribution of the flora of Britain is discussed. So far as East Anglia is concerned there is little evidence that any considerable portion of the flora survived glaciation. The novel suggestion is made, however, that the extensive areas which gradually became available for colonisation on the retreat of the European ice-sheet provided habitats for plants of open communities such as those which to-day are mainly characteristic of cultivated and disturbed soil. The earlier phases of the post-glacial period may, indeed, have been the chief period of the geographical extension of these species. This view may not meet with general acceptance. The species of cultivated land, commonly therophytes, are usually regarded as followers of man. If, in Britain, they were early immigrants in the post-glacial succession, tolerant of the prevailing climatic conditions, they might be expected as early invaders in areas more recently freed from ice. But in such areas, if they occur at all, they are invariably associated with human activity.

In the main portion of Prof. Salisbury's paper the British flora is divided into nine components, defined mainly by the areas in which they occur on the Continent. These components are (a) the alpine, (b) the northern, (c) the southern, (d) the oceanic, (e) the continental, (f) the western-central, (g) the endemic, (h) recent immigrants and (i) generally-distributed species. Four of these (b, c, d and e) are subdivided into eleven elements. The primary groups are clearly more suited to give a truer picture of the British flora in relation to that of the Continent than the types of distribution employed by H. C. Watson, whose treatment was too parochial, but it may be questioned whether the subdivision of some of the components has not been carried too far. The continental-northern element of the northern component must be difficult to separate from the northern-continental element of the continental component. The two elements, in fact, contain a number of overlapping species. Fuller definitions of some of the elements, making clearer where the lines of demarcation are drawn, would have been welcome.

Alpine species are absent from East Anglia, but of the northern component, the arctic, the northern and the continental-northern elements have collectively some 20 species. The southern component is divided into the southern element (18 species), the mediterranean (15 species) and the continental-southern element (66 species). Of the last mentioned group as many as 60 per cent. exhibit within Britain a diagonal limit of distribution in the S.W.–N.E. direction, indicative of their comparative intolerance of oceanic conditions, soil factors apparently playing little part in determining this distribution. On the other hand, the oceanic component, comprising a western element (43 species) and a southern-oceanic element (32 species), possesses a majority of species having a diagonal limit passing in a S.E.–N.W. direction, a distribution again attributed mainly to climatic causes. The continental component comprises 99 species in all, 25 grouped as the steppe element, 44 forming the continental element, and 30 referred to the northern-continental element. The occurrence of steppe species is associated with a combination of low rainfall and favourable edaphic conditions. The northern-continental species grade into the continental-northern element and the reference of some species to one or the other group is a matter of opinion. The western-central component with 11 species is a small ill-defined assemblage, frequently showing local distribution. The distribution of the endemic species, six in number, does not appear to be connected with their presumably recent origin.

Finally, reference is made to a considerable number of species which are recent immigrants. Many of these exhibit discontinuity of distribution, and from a consideration of the group as a whole Prof. Salisbury concludes that it is extremely unlikely that the area occupied can be taken as a criterion of the direction of their immigration or as an indication of the time of occupation. This contention may readily be admitted for species which are adventitious, but

for the native flora as a whole there is some evidence in favour of the view that migratory lines can be traced in relation to the areas occupied by certain species or groups of species. The reviewer believes, also, that the time factor cannot be entirely excluded from problems of geographical distribution, although Prof. Salisbury seems to regard its influence as negligible.

The general conclusion is reached that the climatic factor is the dominant one in determining the distribution of species in Britain, though in some cases this is liable to be modified by edaphic, topographic and biotic conditions. East Anglia itself possesses two strikingly contrasted climatic areas, in which the marked difference in precipitation is accentuated by differences of soil and topography, resulting in the juxtaposition of both continental and oceanic species. Throughout the paper interesting points constantly arise and are too numerous to be dealt with here. The work is, in fact, a very valuable contribution to phytogeography and should be read by everyone interested in the problems of the origin and distribution of the British flora. An attractive and exceedingly useful feature is the large number of maps (106 in all) illustrating the comital distribution, and in some cases the relative abundance, of individual species. Though further field work may result in slight modification of some of the maps, they will long remain a source of great interest and valuable information. The eight plates contain good photographs of species which are rare or are of special interest in the flora of East Anglia. Copies of the paper (price 5/-) may be obtained from the Secretary of the Norfolk and Norwich Naturalists' Society, 31 Surrey Street, Norwich.

<div style="text-align: right">J. R. Matthews.</div>

TWO ELEMENTARY BOOKS ON ECOLOGY

Leach, William. *Plant Ecology for the student of British Vegetation.* Pp. vi + 104, with 6 figures in the text. London, Methuen and Co., Ltd., 38 Essex Street, Strand. Price 3*s*. 6*d*. 1933.

Stork, J. W. and **Renouf, L. P. W.** *Plant and Animal Ecology.* Pp. ix + 197, with 92 figures and photographs in the text. London, John Murray, Albemarle St. Price 5*s*. 1933.

The increasing recognition of the value and importance of ecology to pupils in schools and students at the universities is seen in the publication of such elementary books as the two here noticed.

Dr Leach's book (in Dr de Beer's excellent series of biological monographs—of small size and low price but of excellent quality), though quite simple in treatment and suitable for the beginner, gives a very good conspectus of the problems of British vegetation. In a short space he expounds the principles of the subject from the modern points of view, treating successively of plant communities, ecological factors, and succession. He then deals with the practical study of these in the field, and finally gives a brief sketch of types of British vegetation. The pedological sections are in advance of anything that has yet appeared in an elementary book. We can heartily recommend this little work to the beginner in ecology.

The book by Messrs Stork and Renouf has the admirable ideal of treating animals and plants together, but it may be doubted whether the time is ripe for a work of this design. Not enough is yet known of the actual communities of animals inhabiting different kinds of vegetation, and still less of the interrelations of the animals and plants. The book contains a great deal of good information in a short space—it is in fact a very condensed modern elementary natural history. But there are signs of haste in the preparation (e.g. the occasional miswriting or misspelling of plant names), and in places of a want of sufficiently thorough acquaintance with ecology—at any rate with plant ecology. There are a great number of interesting figures, but not all the reproductions of photographs are as good as they

should be, partly because they are printed on text paper. There is a fascinating frontispiece of "an otter on the alert," standing on its hind legs with an uneasy pose and expression recalling Mr Gluyas Williams' drawings of the middle-class paterfamilias.

A. G. T.

LOCAL VEGETATION AND FLORA

Newton, L. M. *Plant Distribution in the Aberystwyth District, including Plynlimon and Cader Idris.* Pp. 50 with 8 figures and photographs and a vegetation map. Cambrian News, Ltd. Aberystwyth. 1933.

Prof. Newton begins with a brief account of the physiography and geology of the district, and then deals with the principal types of plant community met with, from the seaweeds of the coast to the arctic-alpine vegetation on the summits of the Cader Idris range. She has had the advantage of referring to her own work on the seaweeds, the late Prof. Yapp's on the salt-marshes of the Dovey estuary, which was published in this *Journal* in 1917, an unpublished thesis by S. B. Thomas on the woodlands, an unfortunately unpublished survey by Prof. Stapledon of the hill country behind Aberystwyth, and Mr Price Evans' recent work on Cader Idris, which appeared last year in this *Journal*. From these, supplemented by other observations, it has been possible to put together a very readable account of the vegetation of this beautiful and interesting district.

Lee, John R. *The Flora of the Clyde Area.* John Smith and Son (Glasgow) Ltd. Pp. xvi + 391. Price 7s. 6d. 1933.

This very attractive and useful little book is thoroughly modern in arrangement and treatment, and at the same time remarkably straightforward and easy to use. Dichotomous keys are provided to the families, genera and species, and the diagnoses are clear and simple. The "size" of species adopted is conservative: the author does not err on the side of the recognition of "microspecies." The system employed follows on the whole the sequence of families generally employed in British floras, but the families (unfortunately called "natural orders," a usage which we hoped was diminishing and which nowadays is really indefensibly "provincial") are grouped into orders (here called "groups")—Ranales, Parietales, etc. The apetalous families are distributed among the Archichlamydeae in Chenopodiales and Polygonales following Caryophyllales, and Euphorbiales, Urticales and Amentales following Geraniales and preceding Rosales.

The "Clyde area," i.e. the whole of the land surface draining into the river and firth of Clyde, embraces of course a great range of altitude and habitat, including many high mountains. It is separated into ten divisions, lettered A to J, mostly corresponding with Watsonian vice-counties. Ailsa Craig is added as an eleventh. The distribution of each species is given in terms of these divisions, with localities for the rarer plants. The kind of habitat is briefly given, and frequency is indicated by such terms as "very common everywhere," "common," "frequent," "rare," etc.

Of criticisms, apart from the use of "orders" for families, we have very few. The author's treatment of aliens and casuals is on the whole well judged, but he remarks, rather surprisingly, in the Introduction, that "the Spruce Fir and the Horse Chestnut have as good a right to be regarded as British as have the Sycamore and the Lime." The large-leafed and the small-leafed Limes are unquestionably native in England (which after all is British), and the Sycamore springs from self sown seed everywhere and often establishes itself. It is certainly the best naturalised of alien trees. This is surely not true of the Horse Chestnut, which is practically always a planted tree, nor is it true at all generally of the Spruce, even in Scotland.

A. G. T.

THE MAY ISSUE OF *THE JOURNAL OF ANIMAL ECOLOGY* (VOL. II, NO. 1)

This number contains seven papers, two short notes, fifty short abstracts of British papers on animal ecology, and some reviews. In addition there is a supplement consisting of a long paper by A. J. Nicholson on "The Balance of Animal Populations." This paper summarises previous theories about the nature of the balance of numbers and of fluctuations in numbers, and proceeds to a carefully reasoned analysis (based on mathematical principles) of the author's new theory that the balance of animal numbers depends on the searching for food (i.e. preys, etc.) and the relation of success in searching to resulting densities in the populations of prey and predator or parasite. J. E. Nichols describes and figures climographs for different breeds of sheep in Britain, and applies the conclusions tentatively to forecasting probable favourable climates for certain breeds in Australia and New Zealand. An account of the ecology of grasshoppers on Studland Heath, Dorset, is given by C. and P. Diver. This paper contains also a description of local environmental conditions illustrated by six photographs. W. B. Alexander summarises the literature on previous studies of the rook in Great Britain, and describes his own investigations in the Oxford District. A map of the feeding territories round different rook roosts is an important addition to knowledge of rook ecology. J. M. Winterbottom gives a general picture of the bird communities in Nigeria, together with relative estimates of numbers in different habitats, partly based on counts from trains and partly on sample censuses. Fluctuations in cedar cone crops in Siberia are discussed by A. N. Formosof, who demonstrates the connection between cedar crops and the fluctuations in numbers of red squirrels, by using as an index of crops the periodic migrations of the nutcracker, a bird closely linked ecologically with the cedar. H. F. Barnes continues a series of insect fluctuation studies with an account of the gall midge of meadow foxtail grass and its parasites. T. H. Harrisson and J. A. Moy-Thomas describe the results of a survey of wild mice on St Kilda, after the evacuation of most of the inhabitants, and conclude that the house mouse will die out, but the field mouse is at present abundant and has good prospects.

Short notes deal with censuses of gannets, and a summary of the distribution of the great autumn mortality of swallows in Central Europe in 1931; while reviews include a summary of contents of the *Journal of Ecology* for February, the great crested grebe census enquiry of 1931, McAtee's theories of selection of food by birds, game population research on the partridge, a sand-dune survey in Finland, the coral reef survey of the Great Barrier Reef Expedition of 1928–29, and a new Russian text-book of animal ecology. The present number contains 178 pages (including the 46-page supplement), and 4 plates.

CHARLES ELTON.

MYCORRHIZA AND TREE GROWTH

1. "Reports of Committee on Mycorrhiza in Relation to Forestry." *Brit. Ass. Reports* for 1930, 1931 and 1932.

2. "Mycorrhiza in the genus *Citrus*." M. C. Rayner. *Nature*, **131**, 399, 1933.

These reports, drawn up by Dr M. C. Rayner, summarise certain general features of the mycorrhizal relation in forest trees. One of the original problems presented was the fact that certain areas in the neighbourhood of Wareham and Ringwood proved quite unsuitable for growing various species of pines from seed. The three principal species used, Scots Pine, *P. sylvestris*, Corsican Pine, *P. laricio*, and Maritime Pine, *P. pinaster*, all normally form

mycorrhiza in their natural habitats and it was found that unsatisfactory growth in the area studied was correlated with a complete or nearly complete failure to produce mycorrhiza in the early stages. In the case of Scots Pine, moreover, there was observed a remarkable correlation between vigorous and spontaneous growth in certain localities and the appearance in these localities of sporophores of certain fungi known to be mycorrhiza formers. It appears to be established by the results of detailed examinations that mycorrhizal formation is an invariable concomitant of healthy growth. As two of the species studied, *P. laricio* and *P. pinaster* are exotic, it was necessary to determine whether the failure of the seedlings was due to the absence of appropriate fungi. Apparently both species can form mycorrhizal associations with certain indigenous soil fungi, *P. pinaster* with comparative case, the Corsican Pine with some difficulty. Both species, however, benefit greatly when the soil is inoculated with a small amount of humus obtained from their native habitats. These results were obtained with both field and pot cultures and the improvement is shown in a single growing season. It is not known, however, whether this improvement is due to the introduction of more favourable fungal associates or to other causes. It does appear probable, on the other hand, that the failure of trees to develop is in part due to nitrogen starvation. Experiments with inorganic nitrogenous fertilisers show that it is difficult to improve the growth of the seedlings by this method, owing to serious disturbances in the top-root ratios. The improvement following "native humus" inoculation may, therefore, be due to the introduction of substances or organisms which either directly favour the formation of mycorrhiza, or else which modify the course of organic decomposition in the soil in such a way as to lead to conditions favouring mycorrhiza development. The latter possibility is being studied further by the addition of composts containing various types of organic substance. Its possible existence is, however, indicated by other field and pot studies. For while it is evident that, in the field, certain obvious conditions, such as bad aeration, may prevent the normal establishment of the mycorrhizal relations, yet it is found that the removal of these conditions does not necessarily remove the inhibiting factor. The result of these studies is thus to show the extreme sensitivity of the mycorrhizal relation to the soil conditions and to suggest the possibility that the nature and mode of decomposition of the soil organic matter may be a factor of great importance.

During the course of this detailed work, other facts connected with tree mycorrhiza have come to light. It has been ascertained that certain types of mycorrhiza are associated with vigorous development of young oak trees. In the Forest of Dean, the presence or absence of these types is markedly correlated with the success or failure of oak plantings. It is further pointed out that the unspecialised mycorrhiza known as the Phycomycete type is not only recorded for an enormous number of wild herbaceous species but also for certain crop plants, such as strawberry, sugar cane, wheat and the lychee. Apparently also it is present both in the sweet orange, *Citrus sinensis*, and the sour orange, *C. aurantium*, in the orchards of southern California. In these orchards, some form of nitrogenous manure is practically the only fertiliser employed. Sodium nitrate and other inorganic forms of nitrogen give poor results, but they are highly beneficial if applied with rapidly decomposable organic matter or stable manure.

The suggestion is therefore made that the organic materials provide food for the root fungus and allow of the development of conditions suitable for root infection, a proportion of the metabolised products passing eventually to the root cells during the regular and extensive digestion of the intracellular mycelium. W. H. P.

THE CRUMP COLLECTION OF LANTERN SLIDES, PRINTS AND NEGATIVES OF BRITISH VEGETATION

THIS collection of lantern slides, prints and negatives, generously presented to the Society by Mr W. B. Crump, M.A., of Leeds, was referred to in the Secretary's Report at the last Annual Meeting of the Society (This JOURN. **21**, 224). Mr Crump was one of the pioneers of the study of vegetation in this country in the last decade of the nineteenth century, and later a member of the British Vegetation Committee from which the British Ecological Society sprang—facts which may not be known to some of the younger members of the Society. The making of the photographs which he has now given to the Society has been a labour of love extending over many years, and they include many characteristic views of native vegetation as well as some plant portraits. They are now available for the use of members.

Pending the preparation of a complete catalogue of photographs in the possession of the Society, it may be useful to publish, for the benefit of members, an indication of the nature and scope of the Crump Collection. This consists of about 200 negatives (some 5 × 4 in. and the rest 3½ × 2¼ in.) with corresponding prints (about half with enlargements) and lantern slides.

The photographs are arranged according to the classification of British plant communities used in *Types of British Vegetation*. They include examples of:

Maritime associations, comprising salt marsh and sand-dunes, the former mainly from Norfolk and Hants, the latter from Norfolk, Somerset, Lancs, and Wales.

Fresh-water associations, including floating vegetation, reed swamp and marginal plants (Norfolk, Suffolk, Somerset, Lancs and Yorks).

Peat associations: (1) Fen (Norfolk and Cambs), (2) Lowland heath and moor, (3) Heather moor, (4) Cotton-grass moor, Bilberry moor, Retrogressive moor (Yorks, Derby, Cheshire, Wales, Somerset, Dorset).

Associations of Sandy Soils (Bunter Sandstone and Lower Greensand): (1) *Quercus robur* wood, (2) Oak-birch heath, (3) Lowland heath (Cheshire, Norfolk, Suffolk, Bucks, Surrey).

Associations of Siliceous Soils: (1) *Quercus sessiliflora* wood, (2) *Betula pubescens* wood, (3) Heath pasture (Yorks and Cheshire).

Associations of Calcareous Soils: (1) Beechwood (Sussex, Surrey, Hants, Oxon, Glos), (2) Ashwood on Mountain Limestone (Somerset, Yorks, Derby), (3) Ash-oakwood on calcareous clays, etc. (Cambs, Essex, Somerset, Lancs), (4) Calcicolous scrub and pasture (Chilterns, Surrey, Westmorland, Lancs, Yorks, Derby, Somerset), (5) Limestone pavements (Westmorland, Yorks).

Culture associations: Plantations and hedgerows.

The collection is at present housed at the Department of Botany, Botanic Garden, Oxford, by Mr Crump's desire. Members of the Society may borrow a reasonable number of prints or lantern slides for a limited time on payment of carriage both ways.

Messrs Flatters and Garnett, 309 Oxford Road, Manchester, have a set of negatives from which they are prepared to supply lantern slides to members of the Society only at 1s. 3d. each (ordinary price 1s. 6d.). A catalogue of slides which the firm can supply may be obtained from them.

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

(1) CANADA (COLLABORATOR, J. E. DANDY)

791. Adams, J. "A Bibliography of Canadian Plant Geography, 1921–1925." *Trans. Roy. Can. Inst.* **17**, pp. 267–295. 1930. (1. 202.)

This is a continuation of the Bibliography (dealt with in Abstract **476**) which covered the period up to the end of 1920. The names of authors are arranged alphabetically. At the end of the paper are lists of additions and corrections to the original Bibliography already mentioned.

792. Adams, J. and **Norwell, M. H.** "A Bibliography of Canadian Plant Geography, 1926–1930." *Trans. Roy. Can. Inst.* **18**, pp. 343–373. 1932. (1. 203.)

A further extension of the Bibliography mentioned in the preceding Abstract (**791**). The present contribution is arranged in the same way as the first extension, with lists of additions and corrections.

793. Martin, G. W. "New species of slime moulds." *Journ. Wash. Acad. Sci.* **22**, pp. 88–92, Figs. 1–13. 1932. (1. 204.)

One of the new species is *Amaurochaete trechispora*, described and figured by T. H. Macbride and Martin from Ontario.

794. Victorin, M. "Quelques plantes nouvelles ou reliquales du bassin de la Baie des Chaleurs." *Contrib. Lab. Bot. Univ. Montréal*, **20**, pp. 1–22, Figs. 1–13. 1932. (1. 205.)

In this contribution the author deals with three very interesting plants from the Bonaventure County portion of the Gaspé Peninsula, Quebec. The first is *Aster gaspensis*, described and figured as a new species; this is an addition to a group of Asters (sect. *Fulcrati*) of which the remaining members are confined to the western side of North America. *Gentiana gaspensis* also is described and figured as new; this plant is considered to be the link connecting the northern European and Greenland *G. detonsa* with the western North American *G. Macounii* and *G. tonsa* (a new combination based on *G. detonsa* var. *tonsa*). Both *G. Macounii* and *G. tonsa* are Canadian species. The third plant discussed is referred to *Lathyrus nevadensis*, and is regarded as a relic, for it is the only known eastern representative of a species which is widespread in the Pacific United States. Besides figures of the plants the paper (which is in French) is illustrated with maps showing the geographical relationships.

795. Victorin, M. "Sur quelques ptéridophytes nord-américaines." *Contrib. Lab. Bot. Univ. Montréal*, **21**, pp. 1–7, Figs. 1–3. 1932. (1. 206.)

Lycopodium tristachyum var. *boreale* is described and figured as new from material collected in the neighbourhood of the Great Bear Lake, Mackenzie. *Botrychium minganense*

is recorded from the same region. Victorin discusses the validity of this latter species, and gives a key separating *B. Lunaria*, *B. minganense*, *B. pumicola*, and *B. simplex*. The paper is in French, and is accompanied by maps showing the distributions of *L. tristachyum* (with its var. *boreale*) and *B. minganense*.

796. Davidson, J. "The Flora of British Columbia." *Journ. Roy. Hort. Soc.* **56**, pp. 201–206, Figs. 66–72. 1931. (1. 207.)

In this contribution the author deals only with species of horticultural interest, and describes the habitat conditions under which they grow.

797. Rydberg, P. A. "Taxonomic notes on the flora of the prairies and plains of Central North America." *Brittonia*, **1**, pp. 79–104. 1931. (1. 208.)

This paper is preliminary to the publication of the Flora dealt with in the following Abstract (**798**). It contains notes on nomenclatural problems and changes, together with diagnoses of new species and genera.

798. Rydberg, P. A. *Flora of the Prairies and Plains of Central North America.* Pp. i–viii + 1–969, Figs. 1–600. 1932. (1. 209.)

A complete manual of the flowering-plants and pteridophytes of the states of Kansas, Nebraska, Iowa, Minnesota, South Dakota, and North Dakota, and of southern Manitoba and south-eastern Saskatchewan. Keys are provided, and each species is furnished with an adequate description.

799. Samuelsson, G. "Die Arten der Gattung *Alisma* L." *Ark. för Bot.* **24**, A, 7, pp. 1–46, Figs. 1–3, Plates 1–6. 1932. (1. 210.)

A critical revision (in German) of the genus *Alisma*. According to Samuelsson's arrangement, *Alisma* is represented in Canada by three species, as follows: *A. Plantago-aquatica* (subsp. *brevipes*), *A. subcordatum*, and *A. gramineum* (type and var. *Geyeri*). *A. Plantago-aquatica* subsp. *brevipes* and *A. gramineum* var. *Geyeri* are published as new combinations based on *A. brevipes* and *A. Geyeri* respectively.

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

800. Fourcade, H. G. "Contributions to the Flora of the Knysna and Neighbouring Divisions." *Trans. Roy. Soc. S. Afr.* **21**, pp. 75–102. 1932. (2. 160.)

This is a list of the flowering plants found in the divisions of George, Knysna, Humansdorp, and Uniondale, based chiefly on the collections of the author. New species are described in the genera *Anapalina*, *Tritonia*, *Lachenalia*, *Massonia*, *Ornithogalum*, *Lobelia*, *Prismatocarpus*, *Aster*, *Osteospermum*, *Senecio*, *Cuscuta*, *Cotyledon*, *Heliophila*, *Pelargonium*, *Cyclopia*, *Indigofera*, *Psoralea*, *Vigna*, *Plantago*, *Agathosma*, *Barosma*, *Sutera*, *Solanum*, and *Lachnaea*, and new combinations or new names in the genera *Spiloxene*, *Ficinia*, *Scirpus*, *Panicum*, *Hesperantha*, *Bulbine*, *Dipcadi*, *Haworthia*, *Acrolophia*, *Herschelia*, *Carissa*, *Tylophora*, *Berkheya*, *Pentzia*, *Peyrousea*, *Pteronia*, *Kedrostis*, *Leucadendron*, *Leucospermum*, *Panoramus*, *Protea*, *Cytinus*, *Agathosma*, *Allophylus*, and *Hermannia*.

801. Verwoerd, L. and **du Plessis, S. J.** "Descriptions of some new Species of South African Fungi and of Species not previously recorded from South Africa. IV." *S. Afr. Journ. Sci.* **29**, pp. 313–316. 1932. (2. 161.)

New species are described in the genera *Didymosphaeria, Peronospora, Phoma, Phyllosticta,* and *Stigmatea.*

802. Dirkse–van Schalwyk, Hester A. and **Hector, J. M.** "Studies in Soil Bacteria. I: A preliminary Account of the Distribution of *Azotobacter* in some Transvaal Soils." *S. Afr. Journ. Sci.* **29**, pp. 324–331. 1932. (2. 162.)

Of the Transvaal soils examined 60 per cent. were found to contain *Azotobacter.* The higher counts were found in soils with a high pH reaction; further, these soils had either been irrigated or heavily watered.

803. Henkel, J. S. "The Wattle Bagworm (*Acanthopsyche Junodi* Heyl.): an Ecological Study." *S. Afr. Journ. Sci.* **29**, pp. 355–365. 1932. (2. 163.)

The wattle bagworm causes extensive damage to wattle plantations in Natal. Its natural habitat is the thornveld, zones of distribution varying with climatic cycles. The only important indigenous host plant is *Acacia karroo.* Host trees growing in situations subject to sea breezes are immune from bagworm attack. Ecological study indicates that the insect is more likely to be controlled by attacking its early larval stages, than at any other period of its life history.

804. "Novitates Africanae." *Journ. of Bot.* **71**, pp. 69–73 and 122–125. 1933. (2. 164.)

New species of *Leucospermum, Nivenia, Ornithogalum, Neobakeria, Gethyllis, Morea, Ferraria, Watsonia, Gladiolus* and *Hermas* are described.

(3) AUSTRALIA AND TASMANIA (COLLABORATOR, V. S. SUMMERHAYES)

805. Osborn, T. G. B., Wood, J. G. and **Paltridge, T. B.** "On the Growth and Reaction to Grazing of the Perennial Saltbush, *Atriplex vesicarium.* An Ecological Study of the Biotic Factor." *Proc. Linn. Soc. N.S. Wales,* Sydney, **57**, pp. 377–402, Plates 7–9, 5 Text-figs. December 15th, 1932. (3. 57.)

The investigations described were carried out at the Koonamore Vegetation Reserve, in the north-east of South Australia. *Atriplex vesicarium,* the perennial saltbush, is the dominant plant over the extensive shrub steppe formation that is developed in the north-east of South Australia and many other portions of arid Australia. The community is an open one composed of low-growing bushes with much bare ground between. The plants have usually a number of slender brittle stems branching freely at the base. The leaves are non-cuticularised, tomentose with densely packed bladdery hairs and somewhat succulent, but with a high osmotic pressure. The transpiration rate is low and the leaves are able to absorb moisture from the air with 85 per cent. saturation. The root system is extensive but superficial. Deciduous feeding roots are a feature of the main framework, and the root system is probably non-functional during droughts. During prolonged rainless periods the leaves pass into a state of permanent wilting, which is delayed by their capacity to gain water from damp air. Ultimately they are exfoliated and the plant passes into a leafless state.

The diurnal range of temperature is great and therefore the relative humidity at times of low temperature is surprisingly high. The saturation deficit varies during the day, and when it is low the *Atriplex* leaves absorb water.

The north-east district of South Australia is leased as large sheep stations which are subdivided into paddocks, seldom less than 20 square miles in area. These are provided with one or more watering places. Those portions of a paddock within three miles of water are grazed and trampled by sheep much more intensively than others remote from water which may be seldom or never grazed at all. Four zones of decreasing severity in stock effect can be recognised:

The A Zone, immediately around the watering place.

The B Zone, on main feeding grounds of the sheep.

The C Zone, beyond B, which is only lightly grazed.

The D Zone, still more remote and virtually ungrazed.

Systems of transect lines have been run from several watering places on different stations to secure variation in type of country and management. Along these lines the number of saltbushes and the vegetative vigour of each bush according to a predetermined scale has been ascertained. Transect readings obtained in the D Zone, 3–5 miles from water, provide the standard of the unstocked community.

Compared with the D Zone, the B Zone shows an increase in the number of healthy plants, but no significant difference in the total number of plants. The C Zone shows an increase in the total number of plants and also in the number of wilting plants. This Zone is therefore less healthy than either Zones B or D. This is attributed to the planting of seed by the hooves of sheep and the failure to remove moribund plants by light trampling, thus leading to an overcrowded community in which the competition is unduly severe. Intermittent but heavy stocking seems to be more beneficial to the saltbush for the reasons just given.

806. Cunningham, G. H. "The Gasteromycetes of Australasia. XV. The Genera Mesophellia and Castoreum." *Proc. Linn. Soc. New South Wales*, Sydney, **57**, pp. 313–322, Plate 6. December 15th, 1932. (3. 58.)

Altogether six species are dealt with in this paper. Keys to the genera and to the species of *Castoreum* are given, and also descriptions of all the species.

807. Murray, B. Jean. "A Study of the Vegetation of the Lake Torrens Plateau, South Australia." *Trans. Roy. Soc. S. Austral.* Adelaide, **55**, pp. 91–112, 1 Plate, 1 Text-fig., 1 Map. December 24th, 1931. (3. 59.)

The Lake Torrens plateau lies to the west of Lake Torrens, and consists of flat-topped hills and stony or gibber tablelands with patches of sandhills and clay or loam flats. It is surrounded by extensive loam plains intersected by sand-ridges, salt-water lagoons and freshwater swamps. The whole area lies between the 5 in. and 8 in. isohyets, and is part of Tate's Eremian Region.

An analysis of the flora is given and the relationships of it with those of surrounding districts are discussed.

The various geographic, climatic and edaphic factors influencing the vegetation are described; an analysis of the life forms is given in the spectra of the region and various habitats, and several compound species such as *Atriplex vesicarium* are discussed. The climatic climax for the whole region is an open scrub formation of the myall-mulga-*Myoporum platycarpum* type, with a saltbush-bluebush lower stratum among the larger shrubs that grow among the three main dominants. This climax can only be attained when optimum soil conditions prevail; edaphic or sub-climaxes are developed under other conditions. These associations are described in detail with notes on succession, regeneration, etc. A vegetation map of the district is given.

(7) INDIA, BURMA AND CEYLON (COLLABORATOR, R. J. D. GRAHAM)

808. Parkinson, C. E. "A note on the Burmese species of the Genus *Dipterocarpus.*" *Burma Forest Bulletin,* **27** (Botanical Series, No. 4). 1931. (7. 171.)

Drawings of leaf and fruit and a sketch map showing the distribution of the eleven Burmese species are given with field notes.

809. Macalpine, R. I. "Identification of the Garjans (*Dipterocarpus* spp.) in Cox's Bazar Division." *Indian Forester,* Allahabad, **58,** pp. 359–361, Plates 17–20. July, 1932. (7. 172.)

Distinguishing characters of *Dipterocarpus alatus, D. costatus, D. turbinatus* and *D. pilosus* based on the fruits are described. Field distinctions based on vegetative features and periods of flowering and fruiting are also given. The illustrations include the twigs, flowers and fruits with dissections of the flowers.

810. Parker, R. N. "*Casuarina* root-nodules." *Indian Forester,* Allahabad, **58,** pp. 362–364. July, 1932. (7. 173.)

Root nodules are reported on *Casuarina glauca, C. equisetifolia,* and *C. montana* growing at Dehra Dun from seed not deliberately inoculated. Observations indicate that nodules are necessary for satisfactory growth on ordinary agricultural soils in this locality. A list is given of plants said to have root structures produced by nitrogen-fixing bacteria of the *Pseudomonas radicola* type.

811. Aiyar, T. V. V. "The Sholas of Palghat Division." *Indian Forester,* Allahabad, **58,** pp. 414–432, and 473–486, Map 1. August and September, 1932. (7. 174.)

This is a study in ecology and in sylviculture of the tropical rain forests of the western Ghats. The area described covers 140 square miles on the southern extremity of the western Ghats lying 50 miles inland from the Arabian sea. The western boundary is the Malabar plain stretching to sea-level, the eastern boundary the Carnatic plain. The forest areas, lying in the hills, fall into three natural regions. The northern at an elevation between 4000 and 7000 ft. is traversed by two parallel valleys running north and south; the southern region, elevation 2500–3500 ft. traversed by radiating valleys and a central plateau region at 3000 ft. separating both. Nilgiri gneiss is the main skeleton of the hills, the soil a ferruginous clayey loam generally well drained on the slopes. Rainfall averages 250–300 in. in the northern region, the heaviest falls in the south-west monsoon, in the southern region over 150 in. during both monsoons, the central region has a lower rainfall toward the east and that from the north-east monsoon. Periodicity of growth and reproduction occurs, activity being at a minimum from June to September due to heavy rain and constant heavy cloud, even germination of seeds being retarded. Vegetative activity commences in September–October while flowering starts in November and continues till June. Tropical rain-forest reaches an optimum between 2500 and 3500 ft., passing into monsoon forest below this and merging into sub-tropical evergreen forest above 5000 ft.

Tropical rain forest has a dominant first storey 100–150 ft. high and includes *Cullenia excelsa, Machilus macrantha, Elaeocarpus tuberculatus, E. munroii, Palaquium ellipticum, Mesua ferrea, Calophyllum elatum, Canarium strictum, Dysoxylum malabaricum, Vateria microcarpa, Poeciloneuron indicum, Eugenia* sp., *Heritiera papilio, Chrysophyllum roxburghii, Mangifera indica, Artocarpus integrifolia, Polyalthea coffeoides, Cinnamomum zeylanicum,*

Holigarna arnottiana, H. grahamii, Meliosma arnottiana, Hopea glabra, Litsaea wightiana, Mastixia arborea, Hemicyclia alata, Cyclostemon confertiflorus, Strombosia ceylanica, and *Filicium decipiens.*

The second storey consists of *Myristica laurifolia, Hydnocarpus wightiana, H. alpina, Nephelium longana, Lansium anamalayanum, Garcinia spicata, Garcinia* sp., *Elaeocarpus serratus, Adenochlaena indica, Gomphandra polymorpha, Gordonia obtusa, Eugenia* sp., *Baccaurea courtallensis, Glochidion malabaricum, Canthium didymum, Litsaea stocksii, Scolopia crenata, Xanthophyllum flavescens, Mappia foetida,* and *Actinodaphne hookeri.* Shrubs include *Euonymus angulatus, Agrostistachys indica, A. longifolia, Eugenia munroi, Eugenia laeta, Paramignya armata, Sauropus albicans, Leea sambucina, Saprosma fragrans, Webera* sp., *Clerodendron infortunatum, Macaranga roxburghii, Strobilanthes* sp., *Laportea crenulata, Olea dioica, Linocera malabarica, Callicarpa lanata, Pavetta zeylanica, Vernonia arborea, Lepisanthes deficiens, Turpinia malabarica, Orophea uniflora, Sarcococca brevifolia* and *Croton scabiosus.*

The ground flora is poor including *Heckeria subpeltata, Ochlandra Beddomei, Elettaria cardamomum, Curcuma* sp., and some Araceae. Lianas are represented by *Gnetum scandens, Calamus* sp., *Smilax macrophylla, Elaeagnus latifolia, Derris* sp., *Entada scandens, Senecio araneosus, Thunbergia mysorensis, Paramignya armata, Luvunga eleutherandra, Morinda* sp., and *Fagraea obovata,* an epiphyte. Typical features are the extraordinarily large numbers of species; trees with plank buttresses, prop roots and culiflory.

Eight associations are recognised: (1) *Cullenia-Palaquium,* (2) *Poeciloneuron-Palaquium,* (3) *Palaquium-Mesua,* (4) *Ochlandra-Poeciloneuron,* (5) *Ochlandra-Calophyllum,* (6) *Mesua-Calophyllum,* (7) *Vateria-Cullenia,* (8) *Vateria-Mesua.*

(1) With *Cullenia excelsa* and *Palaquium ellipticum* as dominants is the most widespread and prevails at elevations 2500–3500 ft. in the southern and plateau regions, and in the south of the northern region. Soils are deep and well drained; rainfall heavy. Consociations of *Cullenia* and *Palaquium* occur in patches. A variation with *Mesua* occurs at 3750–5000 ft. in the northern region where local conditions cause a rainfall approximating to its demands.

(2) This association occurs only in the northern region between 3000 and 4000 ft. Dominant species in descending order are *Poeciloneuron indicum, Palaquium ellipticum, Calophyllum elatum, Mesua ferrea.* Soils very damp or marsh, rainfall heaviest. In marshy places with *Ochlandra Poeciloneuron* and *Calophyllum* are dominant trees. In well-drained places and above 3500 ft. *Mesua* appears. Consociations of *Poeciloneuron* occur in patches. Apart from this consociation co-dominant species are *Heritiera papilio, Cullenia excelsa* and *Vateria macrocarpa.*

(3) This association occurs between 3000 and 3750 ft. between (1) and (2). The dominant species are *Palaquium ellipticum* and *Mesua ferrea;* co-dominant are *Calophyllum elatum, Heritiera papilio* and *Artocarpus integrifolia.*

(4) and (5) are localised edaphic climaxes in marshy tracts—*Ochlandra Beddomei* with *Calophyllum elatum, Hopea glabra, Eugenia* sp. and *Bischoffia javanica* characterise the first, while with heavier rainfall *Poeciloneuron indicum* replaces *Calophyllum* in the second.

(6) This association replaces (3) at elevations between 3500 and 4500 ft. where it is widespread. Associates are *Litsaea oleoides, L. stocksii, Gordonia obtusa, Elaeocarpus munroii, Cinnamomum zeylanicum, C. sulphuratum, Eugenia* sp., *Symplocos spicata, Alseodaphne* sp., *Actinodaphne Bourdilloni.* Consociations of *Mesua* and *Calophyllum* are features.

(7) *Vateria macrocarpa* and *Cullenia excelsa* with *Palaquium ellipticum, Mesua ferrea, Calophyllum elatum, Polyalthea coffeoides* as co-dominants occur in the northern region on moist well drained soils with heavy rainfall. *Vateria* consociations are an edaphic climax in this community.

(8) *Vateria macrocarpa,* with *Mesua ferrea* and *Calophyllum elatum* as co-dominants, replaces (7) at 4000 ft. on moist slopes and near streams in the northern region.

Successions are described where regressions have occurred. Regression is greatest after landslips, and on abandoned tea estates. First appear grasses with a species of bracken, colonies of *Wendlandia notoniana*. A ground orchid appears after fires, and in places *Hypericum mysorense* is prevalent. Invaders from the tropical rain-forest follow *Maesa perrottettiana* and *Glochidion malabaricum* followed by consocies of *Gordonia obtusa* and *Symplocos spicata* with a height of 30 ft. Later associes of *Acronychia laurifolia*, *Elaeocarpus munroii*, *Meliosma arnottiana*, *Litsaea stocksii*, *Olea dioica*, *Allophylus cobbe*, *Linocera malabarica* and finally one of the climax communities develops.

In grass land adjoining tropical rain-forest the regression is less severe. *Symplocos spicata*, *Gordonia obtusa*, *Linocera malabarica*, *Croton scabiosus*, *Maesa perrottettiana* and *Acronychia laurifolia* are followed by *Macaranga roxburghii* and *Clerodendron infortunatum*, and later by *Elaeocarpus munroii*, *E. serratus*, *Meliosma arnottiana*, *Canarium strictum*, *Canthium didymum*, *Vernonia arborea*, succeeded by one of the climax communities. On open grass land with shallow rocky soil *Phyllanthus emblica*, *Dalbergia latifolia*, *Sterculia guttata*, *Erythrina indica* first appear followed by *Lagerstroemia lanceolata* and *Sapium insigne*. Later colonies of *Heritiera papilio* are succeeded by *Calophyllum elatum* and *Mesua ferrea* if soil water suffices. In areas in the southern region all timber down to 1 ft. diameter was removed. Exposure killed the remaining advance growth of useful species. Weeds took possession to be followed by *Leea sambucina*, *Trema orientalis* and *Macaranga roxburghii*. Sheltered by these *Calophyllum elatum*, *Artocarpus integrifolia*, *Heynea trijuga*, *Lansium anamalayanum*, *Mesua ferrea*, and *Palaquium ellipticum* have regenerated. Semi-tropical rain-forest in the same region contains a few *Calophyllum elatum* and *Mesua ferrea* among *Artocarpus hirsuta*, *Acrocarpus fraxinifolius*, *Lagerstroemia lanceolata*, *Bischoffia javanica*, *Chukrassia tabularis*, *Cedrela toona*, *Hopea parviflora* and *H. wightiana*. After similar denudation there was a regeneration of light seeded species, e.g. *Acrocarpus fraxinifolius*, *Chukrassia tabularis*, *Cedrela toona*, *Lagerstroemia lanceolata* and *Bischoffia javanica* with seedlings of useless species, e.g. *Trema orientalis*, *Macaranga roxburghii*, *Caesalpinia mimusoides*. In two years these latter dominated the regeneration—a marked contrast to sequence with evergreen species.

Sylvicultural characters of *Mesua ferrea*, *Palaquium ellipticum*, *Calophyllum elatum*, *Acrocarpus fraxinifolius* and *Dysoxylum malabaricum* are given.

812. Hole, R. S. "Sal and its regeneration in the United Provinces." *Indian Forester*, Allahabad, **58**, pp. 433–437. August, 1932. (7. 175.)

Reference is made to Smythies' paper (7. 164), and a plea put forward for the more exact use of ecological terms of classification in Indian forest publications.

813. Parker, R. N. "*Cryptocarya amygdalina* Ness, and *C. floribunda* Ness." *Indian Forester*, Allahabad, **58**, pp. 437–438. August, 1932. (7. 176.)

Descriptions of the main distinctions are given and the distribution of the two species.

814. Parker, R. N. "The genus *Cymbopogon* in north-west India." *Indian Forester*, Allahabad, **58**, pp. 687–689. December, 1932. (7. 177.)

The localities for *Cymbopogon schoenanthus*, *C. jwarancusa*, *C. Parkeri*, *C. distans*, *C. gidarba* are given.

815. Champion, H. G. "The problem of the Pure Teak Plantation." *Forest Bulletin* (Sylviculture Series), **78**, 1932. (7. 178.)

816. Wahid, S. A. "Treatment of Babul (*Acacia arabica*) in Berar." *Indian Forest Records Sylviculture*, Series 17, part 2, 1932. (7. 179.)

817. Millard, W. S. and **Blatter, E.** "Some beautiful Indian Trees." *Journ. Bombay Nat. Hist. Soc.* **34**, pp. 139–140, Col. plate 18, Plate 19, Text-figs. 2. November, 1932. (7. 180.)

Gliricidia maculata is figured and described.

818. Biswas, K. "Glimpses of the Vegetation of South Burma." *Journ. Bombay Nat. Hist. Soc.* **34**, pp. 285, 286, Plates 1 and 2. November, 1932. (7. 181.)

In a brief generalised account of the Tropical Rain Forests of South Burma attention is drawn to their striking similarity with those of Chittagong Hill Tracts and Aracan Sea Coasts.

819. Biswas, K. "Algal Flora of the Chilka Lake." *Mem. Asiatic Soc. Bengal*, Calcutta, **9**, pp. 165–198, Plates 24–32. December, 1932. (7. 182.)

The Chilka Lake is a lagoon directly connected with the sea and also fed by the Mahanadi river system. It is situated on the east coast on the boundary of Orissa and Madras. The area is 350 sq. miles, average depth 6 ft., maximum 20 ft., water temperature 25–35° C. The outlet is salty, the main lake brackish in dry season, but both almost are fresh during and after the monsoon. The climate is tropical, rainfall 45–46 in.

The vegetation of sandbanks is *Crataeva religiosa* with grass and sedge, on rocky islands and promontories *Bambusa arundinacea* on slopes with *Phragmites Karka* at base. Nalbano island, the largest, shows a more or less pure association of *Phragmites Karka*. *Pongamia glabra* forms an association on the north and south of Barkuda island. Submerged phanerogams are *Potamogeton pectinatus* and *Halophila ovata*. In the algal flora *Gracilaria confervoides* is the largest, *Enteromorpha intestinales* forma *cornucopiae*, *E. compressa*, *Grateloupia filicina* occur on vertical rocks with *Polysiphonia subtilissima* below; *Cladophora glomerata* forma *callicoma* grows on rocky foreshore, diatoms are abundant. The plankton is not rich and consists of fragments of the above forms held together by *Lyngbya aestuarii* which is the dominant species, reaching 33·8 per cent. The plankton shows a maximum in September with a smaller rise in March. An impossible comparison is made with the Calcutta salt lakes which differ in being situated in the bed of the Hooghly with no direct communication with the sea, having an area of only 26 square miles, an average depth of 1–3 ft. and being fed by muddy tidal sewage water. The land vegetation of mangroves and marsh forms favour brackish and sea water forms which increase in the dry season. Analysis shows a steady rise in minimum halogen content from February to May. The chief algal feature is a green scum of *Euglena* sp., *Chorella vulgaris*, *Pandorina Morum*, *Arthospira platensis*, *Spirulina major* and *Oscillatoria* species and diatoms, while *Microcystis aeruginosa* colours the water. *Enteromorpha intestinalis* and *Chaetomorpha Linum* occur near edges of pools and *Polysiphonia angustissima* on submerged objects. Descriptions of *Oscillatoria chilkensis* and *O. laetivirens* var. *minima* are given as new amongst notes on 22 forms collected.

820. Biswas, K. "Notes on the organisms in the filtered water of Calcutta." *Journ. and Proc. Asiatic Soc. Bengal* (New Series), **26** (1930), pp. 533–540, Plate 4. December, 1932. (7. 183.)

The occurrence of *Synedra affinis* var. *fasciculata*, *Chorella vulgaris*, *Protococcus viridis*, *Lyngbya ochracea* and *Galleonella feruginea* is recorded.

821. Biswas, K. "The rôle of Aerophilous Algae in producing colour effect on the bark of *Oreodoxa regia* in the Royal Botanic Garden, Calcutta." *Hedwigia*, **72**, pp. 31–41, Plate 1. 1932. (7. 184.)

Scytonema ocellatum, Protococcus viridis, Trentepohlia odorata, T. umbrina and *T. jolithus* var. *bovina* occur and their periodic activity corresponds to the monsoon activity.

(9) CENTRAL AND SOUTH AMERICA (COLLABORATOR, R. C. MCLEAN)

822. Swabey, C. "Some Aspects of Silviculture in Trinidad." *Empire Forestry Journ.* **11**, No. 2, p. 222. 1932. (9. 22.)

The soils of Trinidad, except for a small part of the Northern Range, where there are intrusive and metamorphic rocks, are derived from sedimentary rocks, and vary between light sands and compact clays. The bulk of the forest lands have a rainfall of 75–100 in., with a consistently high (78–100 per cent.) relative humidity. The driest months are February, March and April. There are no hurricanes and the mean annual temperature is 67° F.

The climax vegetation is a gregarious forest association of *Mora excelsa* (80–90 per cent. of the stand). The principal other associations are *Carapa-Lecythis-Sabal*, on clays and "good" soils, and *Carapa-Lecythis-Maximiliana* on poorer sands. There are also small areas of scrub in the north-west and of semi-deciduous forest (*Trichilia-Brosimum* association) in the south.

The chief silvicultural problems are: (1) the regeneration of the mixed forests in the reserves, with the replacement of valueless by valuable species; (2) the regeneration of the gregarious *Mora* forests after more or less intensive logging.

So far the *Mora* forests are virtually unaffected by human activities but the mixed forests have been selectively logged for *Cedrela mexicana* and *Mimusops Balata* and to a lesser degree for some other species.

Soil deterioration, due to intense leaching and oxidation of the surface layers, is very marked in exposed areas and particularly affects the regeneration of *Cedrela*, which is a surface rooting tree. Regeneration of this species depends therefore on the maintenance of a close ground cover.